

Quantifying Novel Ecosystems

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Abstract

The concept of “novel ecosystems” is becoming increasingly prominent in the scientific literature concerning ecology and conservation in the Anthropocene. However, the literature reveals several inconsistent and qualitative framings of the “novel ecosystems” concept, hindering systematic efforts to study or address novel ecosystems. This dissertation quantifies novelty in ecosystems and develops a methodology to identify and predict the emergence of novel ecosystems in dynamic landscapes.

Previous attempts to define novelty have not been widely accepted in the scientific community, impeding its practical application in conservation. The project assessed previous methods to identify their strengths and weaknesses, aiming to develop a new method for successfully quantifying novelty.

Building on the findings from the previous methods, two rigorous metrics were developed. Firstly, we tested a method based on calculating dissimilarity between variables associated with novelty at two time periods to get a total novelty score. A second method using Euclidean distance in principal components analysis (PCA) was developed to measure temporal and spatial novelty by calculating distances between points in PCA space. Crucially, both methods involve biotic and abiotic factors.

Applying these metrics in the United Kingdom (UK) context using data from the British Trust for Ornithology (BTO), AVONET, the UK Centre for Ecology and Hydrology (UK CEH) and the Centre for Environmental Data Analysis (CEDA) across a time scale spanning 1968 to 2011 showed how abiotic and biotic novelty do not reflect the same spatial or temporal patterns. This is demonstrated in another application using data from the Global Biodiversity Information Facility (GBIF) and lepidoptera traits, showing the method’s reproducibility and reliability.

Overall, I advocate for the use and further development of the PCA method to quantify ecological novelty, incorporating both abiotic and biotic variables whilst maintaining flexibility in its application to different scenarios.

Contents

- 1 Literature review - Defining Novel Ecosystems 9**
 - 1.1 Human Impacts 10
 - 1.2 Baselines 11
 - 1.3 Case studies 13
 - 1.3.1 The Green Belt 13
 - 1.3.2 An Abandoned Shrimp Aquaculture Site 14
 - 1.3.3 Endangered Anurans In Novel Forests 15
 - 1.3.4 Conclusions from Case Studies 16
 - 1.4 Conservation Action 16
 - 1.5 Conclusions from the Literature Review 18

- 2 Existing Methods to Quantify Novel Ecosystems 19**
 - 2.1 Indices to Quantify Biotic Novelty 19
 - 2.1.1 Biotic Novelty Index (BNI) 19
 - 2.1.2 Urban Ecological Novelty Index (UNI) and Human Agency Novelty Index (HNI) 24
 - 2.2 Indices to Quantify Abiotic Novelty 26
 - 2.2.1 Standardised Euclidean Distance (SED) 26
 - 2.2.2 Bioclimate Vulnerability Index (BVI) and Naturality Index (NI) 28
 - 2.3 Biotic and Abiotic Indices' Use in the Literature 31

- 3 Testing Existing Methodology 32**
 - 3.1 BNI Calculation 33
 - 3.1.1 Obtaining and Cleaning the Data 33
 - 3.1.2 Distance Matrix (`dist.mat`) 34
 - 3.1.3 Years Since Introduction (YSI) 35
 - 3.1.4 Community Matrix (`com`) 36
 - 3.1.5 Calculating BNI 36
 - 3.1.6 Index Outputs 36
 - 3.2 SED Calculation 39
 - 3.2.1 Obtaining and Cleaning the Data 39
 - 3.2.2 Creating a Function to Calculate SED 40
 - 3.2.3 Index Outputs 41
 - 3.3 Comparing the Results of the BNI and SED Methodologies 44

4	Developing a New Method to Quantify Ecological Novelty	49
4.1	Dissimilarity Metric	49
4.1.1	Methods	49
4.1.2	Results	50
4.2	PCA Metric	53
4.2.1	Methods	53
4.2.2	Results	55
4.3	Discussion on New Methods	58
4.3.1	Dissimilarity Metric	58
4.3.2	PCA Metric	60
4.4	Putting the New PCA Method into Practice	64
4.4.1	Discussion of Results	64
5	Conclusion	69

List of Figures

- 1 Example output of ‘date scenario 2’ reproduced from code provided by Schittko et al. (2020), titled ‘sensitivity to the estimation of mean Archaeobiota residence times’. The x-axis represents the mean residence time of Archaeobiota, and the y-axis represents BNI in the left plot and BNIs in the right. The colour scale represents the proportion of neobiota increasing from green to red. 23
- 2 Urban Ecological Novelty Quadrant. This describes how each value calculated for a particular site relates to the three indices used: UNI, BNI and HNI (Teixeira et al. 2021). Sites in quadrant 1 have low urban ecological novelty and human modification, thus indicating areas that could be used as reservoir sites. Sites placed in quadrant 2A are interpreted as those that have undergone human-induced changes, but the species community has remained relatively the same. Quadrant 2B reflects the opposite pattern to 2A, with low human disturbance but large shifts in the biotic community. Sites in quadrant 3 have high urban ecological novelty and contain novel species communities; therefore, it is likely that restoration to a former condition is unfeasible (Teixeira et al. 2021). 25
- 3 These figures, taken from Radeloff et al. (2015), display global maps of novelty according to the abiotic variables of human population, temperature, precipitation and atmospheric nitrogen deposition. a) shows modern global novelty concerning a historical baseline. b) shows predicted future novelty from a modern baseline (Radeloff et al. 2015). The scale bar on the right shows a logarithm of SED values, with larger values indicating a grid cell that is more dissimilar to the global pool of grid cells. 27
- 4 Results from the analysis in Choi et al. (2021) displaying a) the scoring of sites in North East Asia on the quadrant with the Naturality Index (NI) on the x-axis and the Bioclimate Vulnerability Index (BVI) on the y-axis. b) shows the spatial representation of each quadrant based on the calculated bioclimatic changes between the 2000s and 2050. . . . 30
- 5 Histogram displaying the frequency of species pairs in each Euclidean distance category measuring trait dissimilarity. A high value of Euclidean distance indicates larger trait dissimilarity, whereas a lower value indicates trait similarity. Species pairs are organised into the Atlas period with Time 1 as 1968–72, Time 2 as 1988–91 and Time 3 as 2008–11. 35

6	Maps of Great Britain and Ireland coloured by the standardised Biotic Novelty Index (BNIs) values in 10x10km grid cells according to the Ordnance Survey National Grid (OSGB) coordinates reference system. a) BNIs across the first Atlas period between 1968–72. b) BNIs in the second Atlas period of 1988–91. c) BNIs across the third Atlas period between 2008–11. The scale bar (d) shows values of BNIs indicating the minimum and maximum values across all periods.	37
7	Box plot produced in R displaying the pattern in BNIs values. Note the small change in average values overall, but increasing range in values observed in the third Atlas period (2008–11).	38
8	Map of novelty in the UK in 2011 according to the SED equation from Radeloff et al. (2015) coloured by values of SED provided by the scale bar. The novelty was calculated based on the variables of reduced nitrogen deposition, temperature and precipitation. Grid squares are in a 10x10km resolution with higher values of SED in red and lower values in blue.	41
9	Three maps show the distribution of SED values calculated with individual abiotic variables across the UK. Left: map of SED values when nitrogen deposition is the only variable included. Middle: a map of SED values when temperature is the only variable included. Right: a map of SED values when precipitation is the only variable included.	42
10	Scatter plot of SED values for each grid cell when all variables are included on the y-axis and SED values for each variable on the x-axis. The most prominent relationship is between nitrogen deposition and the total SED values of combined variables.	43
11	Scatter graph displaying the relationship between values of BNIs and SED.	43
12	a) Quadrant schematic displaying how many grid cells are represented by different directions of biotic dissimilarity values. b) Map of the British and Scottish Isles coloured by each 10x10km grid cell's quadrant position on the scatter plot of biotic dissimilarity variables. Yellow represents quadrant 1, blue represents quadrant 2, green represents quadrant 3, and pink represents quadrant 4.	51

13	a) Quadrant schematic displaying how many grid cells are represented by different directions of abiotic dissimilarity values. b) Map of the British and Scottish Isles coloured by each 10x10km grid cell's quadrant position on the scatter plot of abiotic dissimilarity variables. Yellow represents quadrant 1, blue represents quadrant 2, green represents quadrant 3, and red represents quadrant 4.	51
14	a) Quadrant schematic of how each grid cell is influenced by the summed abiotic and biotic dissimilarity values. b) Map of the British and Scottish Isles coloured by each 10x10km grid cell's quadrant position on the scatter plot of total dissimilarity calculated from the sum of the abiotic and biotic variables. Yellow represents quadrant 1, blue represents quadrant 2, green represents quadrant 3, and pink represents quadrant 4.	52
15	Flow chart to aid in the understanding of the PCA method to calculate temporal and spatial novelty using both abiotic and biotic variables. . . .	54
16	A bivariate map to display the temporal trends in abiotic and biotic variables indicated by the Euclidean distances between grid cells at the second and third Atlas period (1991-2011). The boldest coloured cells indicate those with larger abiotic and biotic novelty across this period, and those coloured pale grey represent grid cells displaying less novelty in both variables across this period.	56
17	A bivariate map to display the spatial trends in abiotic and biotic variables indicated by the Euclidean distances to the average in the third Atlas period (2011). The boldest coloured cells represent larger Euclidean distances from the centroid, inferring high spatial novelty for that period. Paler coloured grid cells display shorter distances, inferring less spatial novelty from the average.	57
18	Bivariate map showing the Euclidean distances calculated from the abiotic and biotic PCA across 1970 and 2018. Variables used for the abiotic PCA were maximum and minimum temperature, sunshine hours and precipitation. Variables used for the biotic PCA were moth functional richness, diversity, evenness and dispersion. Note the difference in patterns observed here compared to Figure 16.	65
19	Bivariate map of novelty depicted by the Euclidean distances calculated from the average of all points in the PCA axes. Note the stark differences in novelty hotspots here compared to those in Figure 18.	67

List of Accompanying Material

Attached to this thesis is supplementary material which contains surplus code, graphs and analyses that supplement the main text, referenced throughout the text where relevant as: (see SM). The section numbers in the main text are reflected in the supplementary material for coherence.

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Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as references.

1 Literature review - Defining Novel Ecosystems

The term ‘novel ecosystem’ has been circulating in the literature for about 20 years now. Despite this longevity, there is no universally agreed-upon definition of a novel ecosystem. The most common descriptors used are from Hobbs et al. (2006, 2014), (e.g. Kung 2023; Lindenmayer et al. 2008; Montana et al. 2023; Pieck 2020; Santana 2022). These two definitions differ: Hobbs et al. (2006) define a novel ecosystem as: *“new combinations of species that arise through human action, environmental change, and the impacts of the deliberate and inadvertent introduction of species”*. In contrast, Hobbs et al. (2014) use the following definition: *“abiotic, biotic and social components (and their interactions) that, by virtue of human influence, differ from those that prevailed historically, having a tendency to self-organise and manifest novel qualities without intensive human management”*.

The key difference between these two definitions is the inclusion of novel abiotic components and the self-organisation of novel ecosystems. The former definition is now mostly accepted, as novel abiotic elements are either the initial source of novelty, or a secondary occurrence from the change in species composition (Godoy 2019; Fayle et al. 2015; Seelen et al. 2021) and therefore are not often measured as a symptom of novelty.

Defining novel ecosystems as self-organising also allows ecologists to rule out the classification of urban green spaces as ‘novel’, as these are ecosystems that are designed for a particular purpose and exist under significant human interference (Higgs 2017; Kung 2023). However, some scholars have placed urban environments within the realms of novel ecosystems (Cooper et al. 2024; Vanstockem et al. 2018; Seastedt et al. 2008; Pethiyagoda et al. 2012), including the creation of a methodology surrounding this conception to quantify novelty in urban environments (Teixeira et al. 2021). Some argue against classifying urban environments as novel ecosystems because the former is a direct result of human management and, therefore, could instead be classed as designed ecosystems (Morse et al. 2014; Higgs 2017). Santana (2022) states that a novel ecosystem cannot be categorised into anthropogenic or wild because it is neither; it is a new type of ecosystem completely.

New regimes arising in abandoned human landscapes are a common case study of ecological novelty, and there are numerous examples of species thriving in these ‘unnatural’ areas, including coal mine heaps, offshore oil and gas platforms and quarry lakes (Radosz et al. 2023; Van Elden et al. 2022; Seelen et al. 2021; Cavalli et al. 2022). Case studies such as these will be discussed in more detail below (see Section 1.3).

A characteristic that is often used to define novel ecosystems is irreversibility (e.g. Doley et al. 2012; Dudney et al. 2018; Hallett et al. 2013). However, it remains unknown whether, once this threshold to novelty is crossed, it is possible to return to its historic state. This is one of many unsolved questions within the novel ecosystem concept and perhaps the hardest to answer because it is almost impossible to estimate the stability of future ecosystems, although some have tried to predict future species distributions and climates (Radeloff et al. 2015; Yoshida et al. 2023; Williams et al. 2007). Irreversibility is a quality of novel ecosystems that is often discussed in the literature, with some stating that the path to novelty is one way (Dudney et al. 2018; Hallett et al. 2013; Higgs 2017) and others believing a return to a historic state is possible but with significant conservation effort (Hobbs et al. 2014; Miller et al. 2016). Nonetheless, this is all dependent on the definition of such 'historic' and 'novel' states, which is a challenge in itself and will be discussed further below.

Currently, novel ecosystems consist of many unknowns, but they provide opportunities for research and experimentation (Jimenez et al. 2024; Radeloff et al. 2015; Schittko et al. 2020). What current studies on novel ecosystems have already shown is that we cannot assume that only negative consequences arise from novel conditions, since novelty is not equal to degradation and can often have positive impacts on ecosystem functioning (Kung 2023; Pieck 2020; Jimenez et al. 2024). Therefore, more research is needed in emerging and identified novel ecosystems to strengthen our understanding of resilience and adaptability.

1.1 Human Impacts

To be defined as a novel ecosystem, human impact must be involved in the journey towards novelty, but it is argued whether this impact occurs directly, indirectly or both. Direct anthropogenic drivers of novelty are mostly related to land use change, including land conversion for agriculture (Fayle et al. 2015) and mining (Seelen et al. 2021). These actions often have consequences for abiotic conditions, such as altered soil pH and nutrient concentrations (Kowarik 2011). Indirect anthropogenic causes of novelty are generally related to climate change, such as climate-induced species migration (Ordonez et al. 2024) and environmental change (Radeloff et al. 2015), including changes in seasonal rainfall and temperature patterns (Harris et al. 2018). However, the agency of climate change to generate novelty is complex due to the complicated interactions between multiple climate variables and their temporally and spatially varied effects.

To simplify this system, drivers of novelty could also be categorised into presses

and pulses; terms used by Harris et al. (2018) to describe climate effects. Presses are long-term conditions, such as climate change, and a pulse is a short-lived extreme event, for example, a storm. Both are intertwined and interactive, as are the direct and indirect causes of novel ecosystems. When a pulse occurs over a press, it can cause changes in species composition, richness or dominance. These changes can be irreversible or long-lasting, depending on the effect on the ecosystem, and recovery from an extreme event can be hindered by the frequency of such events. This does not mean that undisturbed ecosystems are more resilient to change than disturbed ecosystems (Harris et al. 2018), which aligns with findings from Radeloff et al. (2015) showing that areas with the highest novelty were not correlated with locations that have experienced the most change.

Climate change is a constant factor in novel ecosystems (a press). Moreover, the climate has been changing throughout Earth's history, including a warmer climate of up to 4°C during the Eemian interglacial period 130,000-116,000 years ago (Reu et al. 2014). Therefore, we could argue that this is not a novel abiotic factor when looking at the climate on a longer timescale. However, the novelty that underlies anthropogenically induced climate change is the rate at which it occurs compared to previous periods of global climate change. Consequently, climate variables should be used to provide an anthropocentric perspective on novelty, to investigate the effect of human impacts driving the appearance of novel ecosystems. This opens up a discussion on feasible baselines and base spaces against which ecological novelty can be quantified.

1.2 Baselines

One of the biggest challenges to defining novel ecosystems is determining a baseline for comparison. What is ecological novelty if we cannot decide on a 'historic' state to refer to? Furthermore, measurements of novelty will not be comparable across or within studies if researchers use different baselines on which to define novelty. Historical or natural and abandoned or modified ecosystems are the baselines suggested by Evers et al. (2018) from which novelty can be compared. This qualitative methodology helps to provide frameworks for understanding environmental change. However, it is broad, subject to researcher bias, and ignores the fact that ecosystems are rarely categorisable into a single state. In contrast, Radeloff et al. (2015) argue that novelty should be viewed through both temporal and spatial lenses. Novelty assessed temporally is based on historical baselines, whereas spatial novelty refers to an ecosystem that is non-analogous to previous ecosystems in the same spatial

context (Radeloff et al. 2015). However, the spatial context within which novelty is measured can vary, with some studies using isolated sites (e.g. Matsui et al. 2012) and others measuring novelty across the entire globe (e.g. Kerr 2025).

The majority of literature surrounding novel ecosystems has used this former method of defining novelty temporally. An example includes Schittko et al's (2020) classification of non-native species into archaeobiota, neobiota and neonatives, determined by their time of introduction by humans. Archaeobiota are non-native species introduced before 1492, neobiota after 1492, and neonatives are species established due to anthropogenic climate change (Schittko et al. 2020; Essl et al. 2019). This methodology necessarily generates an arbitrary baseline of 1492, thus rendering all modern ecosystems novel, with the degree of novelty taken by the proportion of introduced species within that community.

The Anthropocene has been used as a temporal marker to compare ecosystems before and after in multiple studies (e.g. Cavalli et al. 2022; Morse et al. 2014; Ordonez et al. 2024; Fayle et al. 2015). One could argue that the novel ecosystem concept is a direct consequence of the Anthropocene due to the onus on human impacts significantly influencing the environment in its definition. Thus, using the Anthropocene as a baseline to measure novelty appears conceivable. However, there is still debate over when the Anthropocene began: some follow the Great Acceleration of the mid-20th century (Essl et al. 2019); others state around 1800, at the time of the first industrial revolution (Steffen et al. 2011). Roberts et al. (2017) even explained that humans have been influencing tropical forests for a minimum of 100,000 years. This discontinuity in a time point marking the start of the Anthropocene makes quantifying the emergence of novel ecosystems challenging, as there is no unanimously agreed-upon historical baseline to compare to.

Ecological novelty can be viewed from two perspectives: site and organism (Heger et al. 2019). A site perspective defines ecological novelty as a site that is considered novel in comparison to a historical reference point. This approach allows for the classification of novelty by relating it to a known baseline. On the other hand, from an organism's perspective, a novel ecosystem is perceived as an ecosystem that is different from the environment in which it evolved. This perspective helps in understanding how this new environment affects individual species (Heger et al. 2019). One example of an organism-centred approach to understanding novelty is by looking at novel resources: Black Rats (*Rattus norvegicus*) have used anthropogenic resources for centuries now; these resources would have been novel when first encountered, but are not novel to the species now (Valentine et al. 2020). Having the choice of defining novel ecosystems from these perspectives allows for flexibility in the interpretation

of conservation goals for these areas (Santana 2022). Considering the complexity and unpredictability of the emergence of novel ecosystems, a method of defining and quantifying novelty needs to reflect this with context-dependent adaptability.

This prolonged lack of clarification in characterising novel ecosystems suggests that we must move on from discussing the theoretical and work towards creating realistic conservation goals for novel ecosystems. To achieve this, a deeper understanding of how novel ecosystems function, the species interactions within and public perceptions of novel ecosystems is necessary. Thus, conservation case studies within novel ecosystems will be discussed next to offer insight into the real-world implications of defining a novel ecosystem.

1.3 Case studies

It is commonly stated that there remains no land on Earth untouched by human impacts, thus considering all modern ecosystems novel (Seastedt et al. 2008; Radeloff et al. 2015; Lindenmayer et al. 2008). This disheartening concept could discourage any conservation action as environmental change appears beyond our control (Murcia et al. 2014). However, novel ecosystems are more recently being positively discussed, with evidence suggesting that many species are benefitting from new regimes (e.g. Pethiyagoda et al. 2012; Morse et al. 2014; Pieck 2020) and novel ecosystems providing grounds for study and experimentation (Morse et al. 2014). Case studies on both positive and negative effects of novel ecosystems will be explored further in connection with the previous discussion on defining novel ecosystems.

1.3.1 The Green Belt

During the Cold War, a border was enforced that ran the entire length of Germany, splitting it into the capitalist West Germany and the communist East for 40 years. Over this period land surrounding the border became largely empty of people and, as a result, created a refuge for at least 1200 German red-listed species across 146 different habitat types (Pieck 2020). This abandoned landscape has therefore been deemed a novel ecosystem as it contains biotic compositions that did not previously occur (at least, since human occupation). This area is viewed as novel from both a site and organism perspective because the site differs from its historic baseline, and certain organisms did not inhabit this area as it was previously occupied by humans. After the wall fell in 1989, much of this region became protected and is now referred to as 'The Green Belt' due to its ecological significance. It has since been subjected to conservation intervention to maintain this species richness. Interventions include dike

relocation to restore the landscape to its pre-disturbance appearance and working with local farmers to get more land protected and enhance natural areas (Pieck 2020).

This example would be classified as a novel ecosystem arising from an area abandoned by humans, coinciding with Evers et al's (2018) methodology. Therefore, one could determine the degree of novelty with a comparison of biotic and abiotic variables in this area before and after the Cold War, provided sufficient data is available. The abandonment by humans allowed conservationists to carry out restoration work unimpeded to maintain the highly diverse and stable populations that exist in this novel ecosystem.

The Green Belt provides an example of a novel ecosystem with positive effects for biodiversity, as new habitats have become available for organisms to inhabit and utilise, offering new resources. In this circumstance, the best conservation action is to maintain the novel ecosystem, and attempts are being made to enhance it further. These new habitats offer refuge to species in the proximity of urban environments, enhancing landscape connectivity for less mobile taxa.

1.3.2 An Abandoned Shrimp Aquaculture Site

Another example of a novel ecosystem arising from abandonment is in Thailand, where an area of a shrimp farm originally converted from a mangrove forest was abandoned in the 1980s. The indirect human impact of abandonment led to the remaining effluent from the shrimp being deposited, resulting in elevated soil levels, shortening the duration of tidal flooding and depleting the carbon stocks from the now dry and saline soil (Matsui et al. 2012). These novel abiotic conditions enabled highly tolerant species to colonise and prevail, outcompeting the native mangrove species (Morse et al. 2014). Unlike the previous case study, this novel ecosystem is entirely driven by novel abiotic factors that led to a change in biotic composition. In this case, the study organisms are experiencing a novel ecosystem compared to the previous ecosystem state, with abiotic conditions in this area having not been observed previously.

Since abandonment, experimentation has been performed in this novel ecosystem to compare mangrove survival and growth rates at different sediment depths by excavating the sediment and planting native mangrove species *Rhizophora mucronata* and *Bruguiera cylindrica* (Matsui et al. 2012). Sediment was excavated by 25cm, increasing the tidal inundation time to 7597 hours a year from only 463 hours per year. The researchers found that the two native mangrove species grew by twice as much in the restored area compared to the novel areas (Matsui et al. 2012), evidencing how unfavourable the novel abiotic conditions were for the native species.

In this example, restoration efforts were applied to return the site to its historic

abiotic conditions, allowing the native mangrove species to recolonise with aid. However, it is not always feasible to enact such rigorous conservation actions due to time and financial constraints (Hobbs et al. 2006; Hobbs et al. 2014; Seastedt et al. 2008). Furthermore, traditional conservation actions may not be successful as they have not yet been applied to novel ecosystems in different contexts (Seastedt et al. 2008; Doley et al. 2012; Hobbs et al. 2014). Moreover, worsening climate change effects and anthropogenic disturbances may threaten the resilience of restored novel ecosystems, suggesting restoration may not be viable in the long term.

Recovery of a novel ecosystem to its historic state may not always be desirable, as the novel conditions could enhance biodiversity and ecosystem function or both, as seen in the previous example of The Green Belt (Doley et al. 2012; Dudley et al. 2018; Murcia et al. 2014). In these instances, conservation efforts should be focused on maintaining the novel regimes (Lindenmayer et al. 2008; Fayle et al. 2015; Hobbs et al. 2014).

1.3.3 Endangered Anurans In Novel Forests

This case study outlines the effects of land use change on Sri Lanka's anuran populations. Anurans in Sri Lanka are highly threatened, with 20 species now extinct, and 41 of the remaining 91 species classed as endangered or critically endangered. This decline in anurans is mostly attributed to primary forest conversion to agricultural land and urban areas. The highly fragmented landscape consists of primary forest, former tea plantations harbouring secondary forests and active agricultural land. These secondary forests are dominated by introduced plants, creating a novel biotic composition compared to that which previously prevailed (Pethiyagoda et al. 2012).

Interestingly, researchers found that 12 out of the 15 anuran species studied persist in the secondary forest in abundances equal to or greater than those found in primary forests (Pethiyagoda et al. 2012). Moreover, some species of anurans thrive in agricultural land and are only known in areas with anthropogenic activity, whereas other anurans present in these highlands are endangered. It is hypothesised that the endangered species are specialists, dependent on the fragments of their native habitat within the tea plantations. From this, the authors conclude that novel ecosystems can provide novel opportunities for threatened species, but each species reacts differently to novelty. It is suggested that the specialist anurans that are unable to persist in secondary forests should be the focus of conservation efforts (Pethiyagoda et al. 2012). Such efforts could include assisted migration to more suitable habitats.

This example shows how habitat specialists are more threatened by novel ecosystems than generalists because they are less able to adapt to novel conditions (Cavalli

et al. 2022), linking to widely observed patterns that specialised species are often less able to adapt to changing conditions (e.g. Williams et al. 2017). This relationship has been evidenced in another example of novel ecosystems, studying the mutualism between ants and ferns (Fayle et al. 2015). Thus, the research undertaken in this novel ecosystem has identified species of conservation importance and determined suitable refugia in which they can persist.

1.3.4 Conclusions from Case Studies

In the context of these three illustrative examples, it has been evidenced that novel ecosystems appear in areas abandoned by human management, are characterised by novel abiotic and biotic conditions and can provide benefits to certain species. Novel ecosystems often present an opportunity for species whose primary habitats are declining and can be used as habitat corridors to link remaining refugia (Pethiyagoda et al. 2012; Pieck 2020). Thus far, the majority of case studies on novel ecosystems have been in abandoned areas (e.g. Jimenez et al. 2024; Lindenmayer et al. 2008; Mahaut et al. 2020). It is likely this is because defining novel ecosystems using natural and historical baselines presents more challenges, while abandoned landscapes exist on a relatively recent time scale and are thus easier to identify. Many authors recommend we move away from ecological approaches based on natural baselines as novel ecosystems and ecosystem processes are becoming more ubiquitous (e.g. Mahaut et al. 2020; Hobbs et al. 2014; Kung 2023; Lindenmayer et al. 2008). To develop appropriate conservation actions in novel ecosystems, an enhanced understanding of how the ecosystem is impacted by novelty at all levels is required to ensure negative consequences are reduced whilst maximising benefits (Hobbs et al. 2014; Hobbs et al. 2006).

1.4 Conservation Action

Considering the case studies discussed above, the Green Belt and abandoned shrimp farm provide examples of how conservationists have successfully used novel ecosystems to benefit biodiversity (Pieck 2020; Matsui et al. 2012). However, from searching the literature, these exemplify the rare cases where conservation action was feasible in the context of novel ecosystems. Numerous scholars argue that restoring a novel ecosystem to its previous state, as in the case study from Matsui et al. (2012), requires too much time and financial resources (Hobbs et al. 2014; Hobbs et al. 2006; Seastedt et al. 2008). Furthermore, the debate as to whether novel ecosystems can return to

their historic state is ongoing, with some in favour of the idea (e.g. Hallett et al. 2013; Higgs 2017; Kung 2023) and others against it (e.g. Murcia et al. 2014; Lennon 2017).

Before conservation actions can be decided, it is paramount to first identify the effects of novel ecosystems within a particular context. Where biota benefit from the novel conditions, no conservation action may be needed to alter the ecosystem state, but steps may be necessary to maintain the novel regimes (Higgs 2017; Clement et al. 2018). Maintaining the novel ecosystem can benefit the current species present and also provide habitat resources that act as suitable replacements for traditional habitats lost to degradation (Valentine et al. 2020).

An example of an alternative habitat provided by a novel ecosystem is for the Knysna Seahorse (*Hippocampus capensis*). This endangered seahorse preferentially selects the novel habitat of rock-filled wire cages over its diminishing traditional eelgrass habitats when offered both during behavioural experiments (Valentine et al. 2020). The novel abiotic conditions provided by the wire cages allow the seahorse to persist within its threatened habitat and, therefore, should be protected and maintained. Similarly, novel ecosystems created by sand and gravel mining have become important habitats for the threatened Least Terns (*Sternula antillarum*) and Piping Plover (*Charadrius melodus*) in Nebraska, USA. As these sites are declining and frequently replaced by modern mines (which have fewer nests recorded in them compared to traditional mines), the recovery and management of these endangered species engenders an interesting debate for the future of the Piping Plover and Least Terns and their relationship with the human environment (Jorgensen et al. 2021).

Despite the benefits that novel ecosystems can provide to species, there is also a plethora of case studies exemplifying the negative consequences of crossing the threshold to novelty (e.g. Gawel et al. 2018; Strayer 2010). One such well-known example is in coral reef habitats: specifically, the Indo-Pacific coral triangle that contains a third of the global coral reefs (Burke et al. 2012). This biodiverse ecosystem is threatened by the novel abiotic conditions of increased water temperature and decreased pH (Radeloff et al. 2015). Moreover, pollution, overfishing and coastal development pose additional threats to the Coral Triangle (Burke et al. 2012). These novel conditions are predicted to continue changing through to 2100 (Hoegh-Guldberg et al. 2007), and coral is unlikely to be able to adapt to these changes quickly enough, with negative effects including stunted growth rates and reduced reproductive capacity among others (Radeloff et al. 2015). This novel ecosystem poses a great challenge to conservationists, as marine ecosystems are often more difficult to manage due to the unpredictability and complex relationships between contributing factors.

The suitable conservation actions for coral reefs are unclear, as are actions for novel

ecosystems. Many argue that current conservation frameworks are rendered useless in the face of novel ecosystems (Seastedt et al. 2008; Higgs 2017; Radeloff et al. 2015; Hobbs et al. 2006), calling for new methods that are adaptive and open-ended to account for further change (Lindenmayer et al. 2008; Morse et al. 2014; Seelen et al. 2021).

1.5 Conclusions from the Literature Review

A conservation framework for novel ecosystems should be flexible and tailored to specific contexts. It should prioritise identifying and addressing ongoing risks to ecosystem health, the services these ecosystems provide, and the interactions among species. (Dudney et al. 2018; Evers et al. 2018; Lennon 2017; Lindenmayer et al. 2008). For this to be achieved, a thorough understanding of the aforementioned processes is required via empirical research in novel ecosystems. However, this would be time and resource-intensive, which may be too time-consuming to provide short-term benefits to the ecosystem during this period of unprecedented change.

Therefore, what is urgently needed is a method to identify and measure novel ecosystems. There have been multiple examples of authors addressing the need for a quantitative methodology to define novel ecosystems (e.g. Kennedy et al. 2018; Hobbs et al. 2009; Godoy 2019). Statistical methods to quantify novelty have been attempted so far (e.g. Schittko et al. 2020; Radeloff et al. 2015), but these are yet to be widely used by ecologists for conservation purposes and remain mostly theoretical. Furthermore, these few attempts fail to combine both key aspects of novel ecosystems: biotic and abiotic factors. These existing methods of quantifying novelty will be a key focus of discussion in the remaining text.

A metric which incorporates both abiotic and biotic factors, alongside being adaptable to different variables and scenarios, would allow conservationists to make informed decisions about appropriate actions to take in the context of novel ecosystems. In addition, having a quantitative method to define novelty will allow it to be viewed as a continuum rather than a qualitative dichotomy (Miller et al. 2016; Radeloff et al. 2015; Santana 2022). Understanding the novelty of an ecosystem enables inferences to be made about the functioning of this ecosystem and its impacts on species interactions, to better direct conservation action.

2 Existing Methods to Quantify Novel Ecosystems

To successfully apply conservation strategies to novel ecosystems, it is essential to first identify what qualifies as a novel ecosystem. Additionally, it is important to assess how different this ecosystem is compared to a predetermined baseline. This quantification of novelty is something that has been frequently advocated in the literature (e.g. Hobbs et al. 2009; Murcia et al. 2014). Novelty should also be understood as a continuum rather than in categorical terms (Schittko et al. 2020; Radeloff et al. 2015), so the extent of novelty can be calculated in a given area to suggest viable conservation implementations based on the findings.

This is important for applied ecologists, stakeholders and policymakers who need clarification on the status of ecosystems in order to direct funds and action. As discussed above, transformation to a novel ecosystem brings certain unknowns, including how ecosystem processes, functions and patterns are impacted (Kompala-Baba et al. 2023; Dudley et al. 2018; Fayle et al. 2015). Therefore, by first identifying the degree of novelty in an ecosystem, further research can subsequently be conducted to fully understand its novel attributes. This will help answer important questions about novel ecosystems, their capacity to sustain biodiversity, and their stability regarding further change. For example, it is vital to realise if these ecosystems have inherent resistance to disturbances, which would then require little conservation effort to ensure the ecosystem's long-term stability (Harris et al. 2018; Hobbs et al. 2014; Montana et al. 2023).

Finally, a methodology to quantify novel ecosystems must incorporate how novelty interacts on variable spatial and temporal scales. This is especially important as novelty can be viewed from different perspectives, as Heger et al. (2019) suggests. Having a diverse metric that can be applied in various scenarios will enhance the field's understanding of the implications for the site and the organisms present in the novel ecosystem. To date, a limited number of metrics have attempted to measure novelty using biotic and abiotic variables independently. Below, I will expand on several of those metrics, followed by empirical testing.

2.1 Indices to Quantify Biotic Novelty

2.1.1 Biotic Novelty Index (BNI)

One attempt to quantify novel ecosystems is the Biotic Novelty Index (BNI) proposed by Schittko et al. (2020). This method comprises temporal coexistence, relative abundance and trait dissimilarities between species pairs to reflect the biotic novelty

of a community in a particular spatial location based on colonisation by novel species (Equation 1). It can be used to quantify novelty across space and time, the latter by comparing the same geographic point at different moments in time, and the former by comparing different sites at the same time.

$$BNI = \sum_{i=1}^{s-1} \sum_{j=i+1}^{s-1} d_{ij} \times c_{ij} \times p_i p_j \quad (1)$$

Equation 1 displays the Biotic Novelty Index (BNI) where d_{ij} is a matrix that comprises distance measures between species i and j in a particular location. This could be trait distance or phylogenetic distance, calculated with Gower or Euclidean distance depending on the variable of choice. c_{ij} refers to the coexistence coefficient of species i and j temporally, calculated from the residency time of each species in that site, represented by a matrix of the pairwise coexistence times of species present. $p_i p_j$ is the relative abundance of species pairs within the given community. This $p_i p_j$ coefficient is optional as it requires abundance data, which is often difficult to source for many taxonomic groups; therefore, if presence-absence data is used, $p_i p_j$ can be removed from the calculation (Schittko et al. 2020). The term s is not defined by Schittko et al. (2020); however, after a detailed review (of both text and code), we summarise that s is likely to be the total number of species within the site of interest for which the BNI is being calculated. Note an error spotted in the original formula provided by Schittko et al. (2020), where the inner summation stops at $s - 1$ when this should in fact be just s to account for all species in the upper triangle. The corrected formula is shown in Equation 2.

$$BNI = \sum_{i=1}^{s-1} \sum_{j=i+1}^s d_{ij} \times c_{ij} \times p_i p_j \quad (2)$$

This equation may seem familiar to ecologists as it has been adapted from Rao's quadratic entropy (Rao's Q, also represented by FD_Q), a metric used to measure functional diversity (Equation 3). BNI can be standardised about Rao's Q to produce BNIs (Equation 4).

$$FD_Q = \sum_{i=1}^{s-1} \sum_{j=i+1}^s d_{ij} \times p_i p_j \quad (3)$$

Equation 3 shows Rao's quadratic entropy (Rao's Q); with s being the total number

of species and the terms d_{ij} and $p_i p_j$ having the same meaning as in the BNI in Equation 2 (Rao 1982). The novelty metric connected to Equation 3 is BNIs (standardised BNI) and is defined by Equation 4 below.

$$BNI_s = BNI/FD_Q \quad (4)$$

BNIs represents the standardised form of the Biotic Novelty Index (BNI) when integrated into Rao's Q. The BNI is divided by Rao's Q to obtain a clearer picture of how novel the species in a community are taking into account its overall functional diversity (Rao's Q is denoted as FD_Q in Equation 3) (Schittko et al. 2020).

Standardised BNI (BNIs) is more useful for ecological interpretation than standalone BNI. The results from the simulations conducted by Schittko et al. (2020) are more intelligible when focusing on BNIs instead of BNI. One reason for this is that BNIs and the proportion of introduced species or 'neobiota' can both be bound between 0 and 1 and therefore can be correlated against one another. BNIs values of 0 mean that the community consists entirely of native species, and values nearer to 1 indicate the community is composed completely of novel species. Unscaled BNI does not have an upper bound, but can be modified by scaling the trait distances if BNIs is not going to be calculated.

The inclusion in the metric of a distance measure (d_{ij}) to assess functional traits provides an effective method for evaluating the impact of novelty in ecosystems. This approach aids in illuminating how the introduction of new biota may influence overall ecosystem functioning. By quantifying the change in functional traits within and across sites using the Biotic Novelty Index (BNI), it is possible to gain preliminary insights into the impacts of biotic novelty, enhancing our understanding of ecosystem dynamics.

The BNI equation incorporates the term c_{ij} into FD_Q (Equation 3). This term represents the temporal coexistence of species i and j , highlighting how these species interact over time. This allows for novelty to be defined within a timescale, given by the maximum and minimum residence times of each species. c_{ij} is calculated using residence times with the formula below (Equation 5 and 6).

$$r'_i = \frac{r_i}{r_{\max}} \quad (5)$$

$$c_{ij} = 1 - \min(r_i, r_j) \quad (6)$$

To begin the BNI calculation, the normalised residence time, r'_i , needs to be calculated using the residence time of species i (r_i) and the maximum residence time for all species (r_{max}), measured in years (Equation 5). Residence time is calculated by the elapsed time of species occurrence since its introduction. For native species, the original authors classify this as the beginning of the Columbian exchange - the year 1492 (see in-text discussion below), and the dates of introduction for non-native species will need to be sourced. This can then be used to produce Equation 6: the temporal coexistence coefficient c_{ij} , using the maximum and minimum residence times of species i and j with 1 representing the year for which novelty is being assessed (Schittko et al. 2020).

Applying a temporal aspect to quantifying ecological novelty is vital, especially considering the number of authors who have called for a metric with this capability (e.g. Kennedy et al. 2018; Hobbs et al. 2009; Godoy 2019). Moreover, the authors suggest using the beginning of the Columbian exchange as a temporal marker if the exact time of introduction is unknown (following Schroeder's three-level classification of plants (Schroeder 1968). Species present in the study area before 1492 are referred to as 'archaeobiota'. Those that appear after 1492 are called 'neobiota', while species introduced since the Anthropocene (here defined as halfway through the 20th Century) are referred to as 'neonatives' (Schittko et al. 2020). This straightforward categorisation into periods makes this metric adaptable for application in numerous contexts, particularly if exact introduction dates are unknown.

Furthermore, the temporal measurement of novelty is inherently based on the maximum coexistence time between two species pairs. Thus, if comparing two time periods within the same analysis, the novelty in the community is compared to this implicit baseline and to each other. However, this could lead to a limitation of the metric's accuracy in defining novelty when attributing general introduction dates to species in the study community. Moreover, this is a major oversimplification of the complexity of ecological systems as the biotic composition of an ecosystem is constantly in flux due to migration, succession and introductions (Godoy 2019; Hallett et al. 2013; Murcia et al. 2014). Therefore, identifying the time of introduction for certain species can prove difficult.

The simulations discussed in Schittko et al. (2020) were successfully reproduced using the R code provided by the authors. When running the simulations that involved

varying dates of species introduction, the graphs plotted from the given code provide limited information regarding the outputs of the Biotic Novelty Index (BNI) and the standardised BNI: BNIs. As the mean residence time of archaeobiotia increases, the BNI and BNIs values of that community decrease ever so slightly. It can also be interpreted that BNI and BNIs are higher when there is a larger proportion of neobiota, compared to lower biotic novelty when the community consists of 0 neobiota (Figure 1). Further tests would be required to understand how significant the change in the BNI values is due to the alteration of residence times and the subsequent effects on functional diversity.

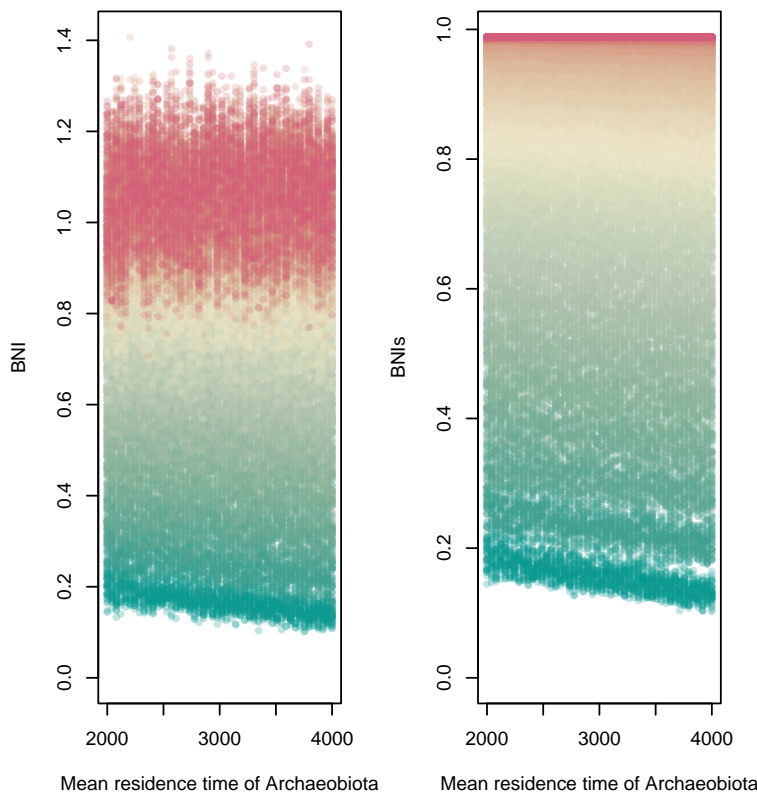


Figure 1: Example output of ‘date scenario 2’ reproduced from code provided by Schitko et al. (2020), titled ‘sensitivity to the estimation of mean Archaeobiotia residence times’. The x-axis represents the mean residence time of Archaeobiotia, and the y-axis represents BNI in the left plot and BNIs in the right. The colour scale represents the proportion of neobiota increasing from green to red.

An integral limitation in this methodology is its specific data requirements (dates of species introductions, abundances and trait measures), restricting its ability to be used for less well-studied groups. Moreover, measuring ecosystem novelty based on biotic variables alone is not fully representative of the state of this area, as ecosystems are influenced by a multitude of factors, both biotic and abiotic, including invasive species,

weather events and land-use change (Kung 2023; Harris et al. 2018; Pethiyagoda et al. 2012). Therefore, to accurately quantify novelty, abiotic factors must be included as key determinants of ecosystem function and resilience.

2.1.2 Urban Ecological Novelty Index (UNI) and Human Agency Novelty Index (HNI)

The Biotic Novelty Index (BNI) has been integrated into the Urban Ecological Novelty Index (UNI) (Teixeira et al. 2021), where it is used as an additional dimension alongside variables of human agency to evaluate ecological novelty in urban spaces. This index is intended for application in urban environments, although this methodology could be adapted for different environments. UNI is the combination of the calculated normalised means of BNI values for the focal taxa in the site of interest and another new index: the Human Agency Novelty Index (HNI). HNI is calculated by summing the novelty of each variable in the ecosystem using a score system. Variables for HNI can comprise momentary, past to present or ongoing human agency; details of the research methodology needed for selecting appropriate variables are provided in Teixeira et al. (2021). Categorical human agency variables are assigned 0 for low, 0.50 for medium and 1 for high levels of novelty; continuous variables can be used in their decimal value (Equation 7).

$$HNI = score\ of\ variable_1 + \dots + score\ of\ variable_n \quad (7)$$

Equation 7 displays the formula to calculate the Human Agency Novelty Index (HNI) as the sum of novelty scores for each variable (Teixeira et al. 2021).

The flexibility in the choice of variables is appealing as it does not limit data requirements and creates adaptability in the application of this metric. However, due to this methodology, comparing the output of HNI values across different studies and sites provides limitations, as there could be many variables with low novelty summing to give a high HNI score or few variables with high novelty leading to the same score, creating a challenge in identifying the main drivers of novelty. Moreover, the scoring system is highly subjective as each user can choose different variables and assign them different scores of novelty; thus, it is neither reliable nor reproducible.

When computing the Urban Ecological Novelty Index (UNI) on a site-by-site basis, values of UNI can then be assigned a position in an Urban Ecological Novelty Quadrant (Teixeira et al. 2021) (Figure 2).

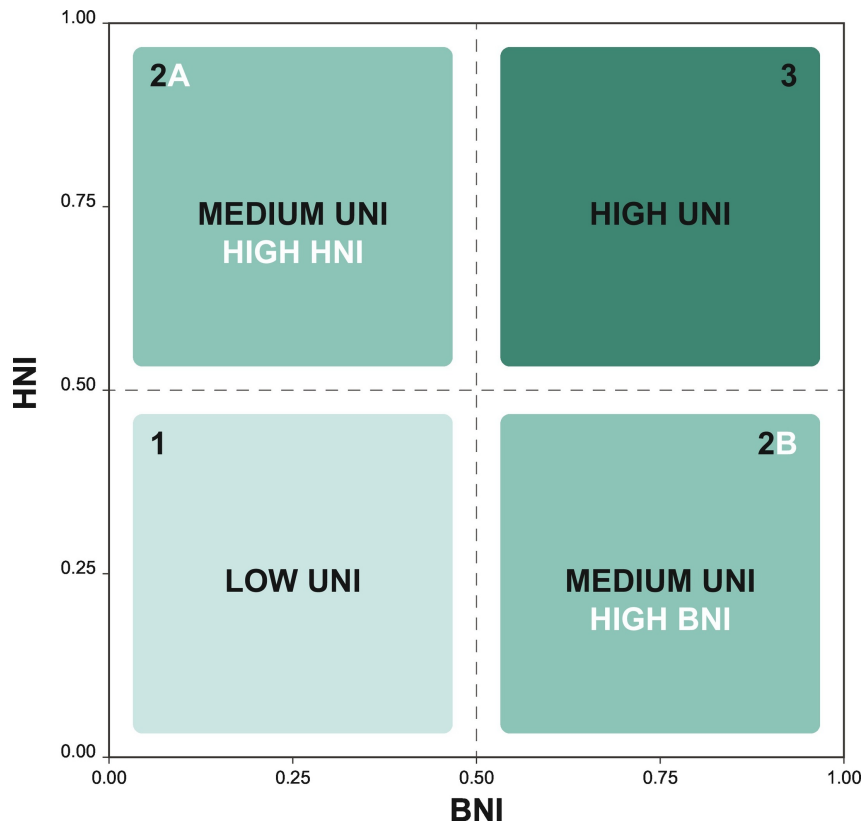


Figure 2: Urban Ecological Novelty Quadrant. This describes how each value calculated for a particular site relates to the three indices used: UNI, BNI and HNI (Teixeira et al. 2021). Sites in quadrant 1 have low urban ecological novelty and human modification, thus indicating areas that could be used as reservoir sites. Sites placed in quadrant 2A are interpreted as those that have undergone human-induced changes, but the species community has remained relatively the same. Quadrant 2B reflects the opposite pattern to 2A, with low human disturbance but large shifts in the biotic community. Sites in quadrant 3 have high urban ecological novelty and contain novel species communities; therefore, it is likely that restoration to a former condition is unfeasible (Teixeira et al. 2021).

The UNI would need to be applied at multiple time points and spatial locations to display temporal and spatial trends. To visualise the output of the calculation for one location at one time point, the quadrant can be used for the interpretation of the results within the context of BNI and HNI. Placing results in the quadrant provides information regarding what is influencing urban ecological novelty: human agency, biotic novelty or both. As this index is intended for urban environments, the human agency dimension is weighted equally to biotic novelty (Teixeira et al. 2021). However, further in-field analysis is necessary to fully understand the drivers of novelty in this area for actionable results to be utilised by stakeholders.

The Urban Ecological Novelty Index (UNI) has yet to be used in the current literature, most likely due to its problematic methodological design. Firstly, the UNI

is an index consisting of indices, meaning it depends on BNI being reliable in itself, of which the limitations have already been discussed. Secondly, the scoring system of categorical variables is restrictive and subjective, thus likely to succumb to researcher bias. Moreover, scoring variables in degrees of novelty contradicts the point of creating a novelty index because the novelty has already been decided by the researcher. A third point is that the UNI combines human agency and biotic novelty, each with equal influence over this novelty metric. However, in certain urban environments, human agency may have a greater influence on creating novelty, in which these two factors should not be equally weighted. Finally, categorising variables of human agency into momentary, past to present or ongoing is also subjective and difficult to define as ecosystems are subjected to constant ‘presses’ and ‘pulses’ from multiple factors (Harris et al. 2018).

This method may not yet have been applied in conservation contexts due to its fairly recent publication date (Teixeira et al. 2021). However, it is also likely that the method has not been used due to the constraints of the methodology explained above.

2.2 Indices to Quantify Abiotic Novelty

2.2.1 Standardised Euclidean Distance (SED)

One key attempt to measure ecosystem novelty with abiotic factors was by Radeloff et al. (2015).

In their paper, they propose a method that uses standardised Euclidean distance (SED) to measure the dissimilarity between 0.5° resolution grid cells at ‘historical’, ‘present’ and ‘future’ time points to quantify how the variables of human population, temperature, precipitation and atmospheric nitrogen deposition contribute to ecological novelty globally (Equation 8). Here, “historical” refers to the late 19th C to early 20th C, ‘present’ to the late 20th C to early 21st C, and ‘future’ to any time points beginning after the mid 21st C.

$$SED_i = \sqrt{\sum_{k=1}^n \frac{(b_{ki} - a_{ki})^2}{s_{kt}^2}} \quad (8)$$

Equation 8 shows the calculation of the SED where k is the index of the abiotic variables and n is the number of abiotic variables. The term a_{ki} refers to the grid cell i at the baseline time point (a) with the value of variable k ; b_{ki} refers to the same grid cell but at the time point where novelty is being assessed. s_{kt}^2 represents the variance (S^2)

of variable k across all grid cells at the baseline time point (t) used to standardise all variables to a common scale (Radeloff et al. 2015).

If the aim is to assess present levels of novelty, grid cell values b_{ki} would be based on the present period, whereas to predict future novelty, b_{ki} would be taken from a dataset containing future projections. Global novelty can then be determined by quantifying the minimum SED (SED_{min}) between the future grid cell values and the pool of baseline grid cells (Figure 3). A SED_{min} of 0 indicates that the grid cell is analogous to its baseline version. Increasing SED_{min} represents more dissimilarity between that grid cell and its most recent analogue (Radeloff et al. 2015).

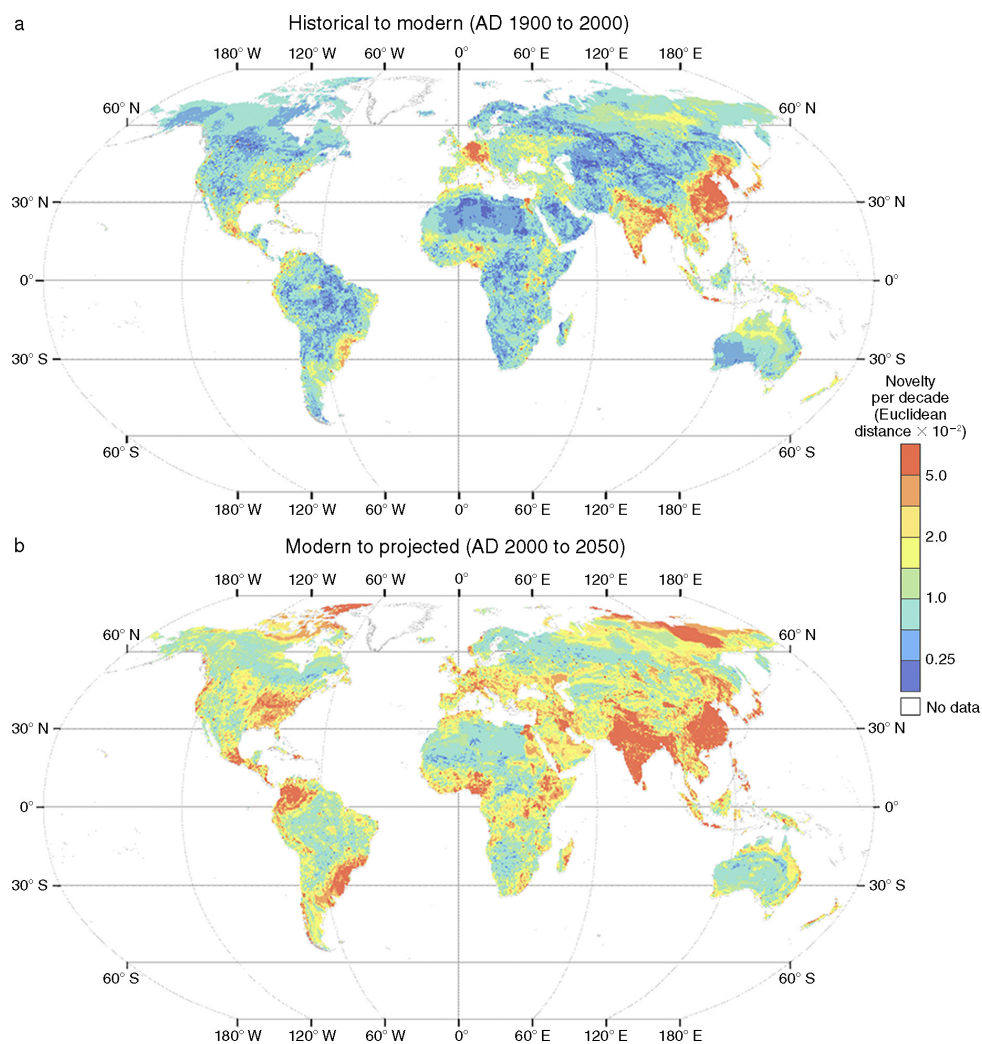


Figure 3: These figures, taken from Radeloff et al. (2015), display global maps of novelty according to the abiotic variables of human population, temperature, precipitation and atmospheric nitrogen deposition. a) shows modern global novelty concerning a historical baseline. b) shows predicted future novelty from a modern baseline (Radeloff et al. 2015). The scale bar on the right shows a logarithm of SED values, with larger values indicating a grid cell that is more dissimilar to the global pool of grid cells.

Note that the SED formula from Radeloff et al. (2015) resembles that of the general standardised Euclidean distance formula but has a few discrepancies; one of which is the inclusion of the component j in the distance measure but its lack of appearance in the squared standardised distance. We argue that this is more likely a type error on the author's behalf, since the term j is not needed in this formula, as the same grid cell (i) is being compared at different time points (a and b). If anything, Equation 8 should be calculating SED_{iaib} because the SED measures the distance in variable k across time points a and b in grid cell i . For this reason, we choose to present the SED formula above in its correct form (Equation 8).

A key advantage of this formula is its applicability to global distribution, as demonstrated by Radeloff et al. (2015). This is useful for the visualisation of current and predicted novelty on a large spatial scale and provides an accessible way to assess where novelty poses the most threat. Interestingly, the findings were that nitrogen deposition and temperature were the most influential predictors of future global novelty (Radeloff et al. 2015). More recently, Lugo and colleagues adapted this formula for biotic variables, using native and naturalised species in tropical forests, due to the lack of abiotic data available for this region (Lugo et al. 2020). The next step for this method is to see how different variables, abiotic and biotic, affect novelty across the globe.

2.2.2 Bioclimate Vulnerability Index (BVI) and Naturality Index (NI)

The Bioclimate Vulnerability Index (BVI) serves a similar purpose to the previous metric discussed by Radeloff et al. (2015). Using bioclimatic maps and general circulation models (GCMs) under representative concentration pathway 8.5 (RCP 8.5) scenarios, the authors mapped past, present and future bioclimatic maps of North East Asia. Using these models collectively, the bioclimatic vulnerability was indexed to record where biodiversity may need support to withstand future climate change (Choi et al. 2019).

The Bioclimatic Vulnerability Index (BVI) is calculated by comparing the novel climate distribution to a baseline distribution (Equation 9). When values of BVI are standardised using the total mean and standard deviation, the output of BVI can be bound between -1 and 1 , interpreted as < -1 for a highly stable bioclimate, $-1 \sim 0$ as stable, 0 to 1 for vulnerable bioclimates and values > 1 are highly vulnerable. This is calculated using the difference between the climate distribution area and the rate at which it is moving. Moving speed is interpreted as how far the density centre of this particular climate zone has moved over time (Equation 9) (Choi et al. 2019).

$$BVI = \frac{\text{Moving Speed}}{\text{Future Distribution Area / Current Distribution Area}} \quad (9)$$

To understand the vulnerability of each zone to climate change, a Naturality Index (NI) was created to include the proportion of natural habitat in each bioclimatic zone (Equation 10) (Choi et al. 2019). It is important to understand where bioclimatic novelty could be most impactful on biodiversity to define and prioritise appropriate conservation actions. The values of the Naturality Index (NI) are complex and cannot be interpreted straightforwardly, as they reflect various factors that contribute to changes in natural areas at different intensities. Therefore, a low NI value cannot be solely attributed to habitat destruction, and a higher value does not necessarily indicate that restoration is taking place (Choi et al. 2019). Further investigation is needed to understand these nuances. Equation 10 shows how to calculate the Naturality Index (NI) described by Choi et al. (2021) as a way of including the degradation of natural zones due to climate change, and urban and agricultural expansion.

$$NI = \frac{\text{Area of Natural Habitat}}{\text{Total Area of each Bioclimatic Zone}} \quad (10)$$

Values recorded for NI, alongside BVI, can be expressed graphically using quadrants to prioritise sites for suitable conservation action (Figure 4). A detailed description of the meaning of quadrant position is provided in Choi et al. (2021). The first can be interpreted as species being heavily impacted by climate change, with an emphasis on maintaining a high level of natural habitat. Areas in the second quadrant are equally as affected by climate change as those in quadrant one; however, significant conservation efforts will be needed to restore the low amount of natural habitat area. Sites in the third quadrant will experience stable bioclimates but have few natural areas remaining, indicating restoration is needed as these sites could be refuges for range-shifting species. The fourth quadrant describes areas under stable bioclimates with large natural areas, suggesting protected areas would be successful here (Choi et al. 2019).

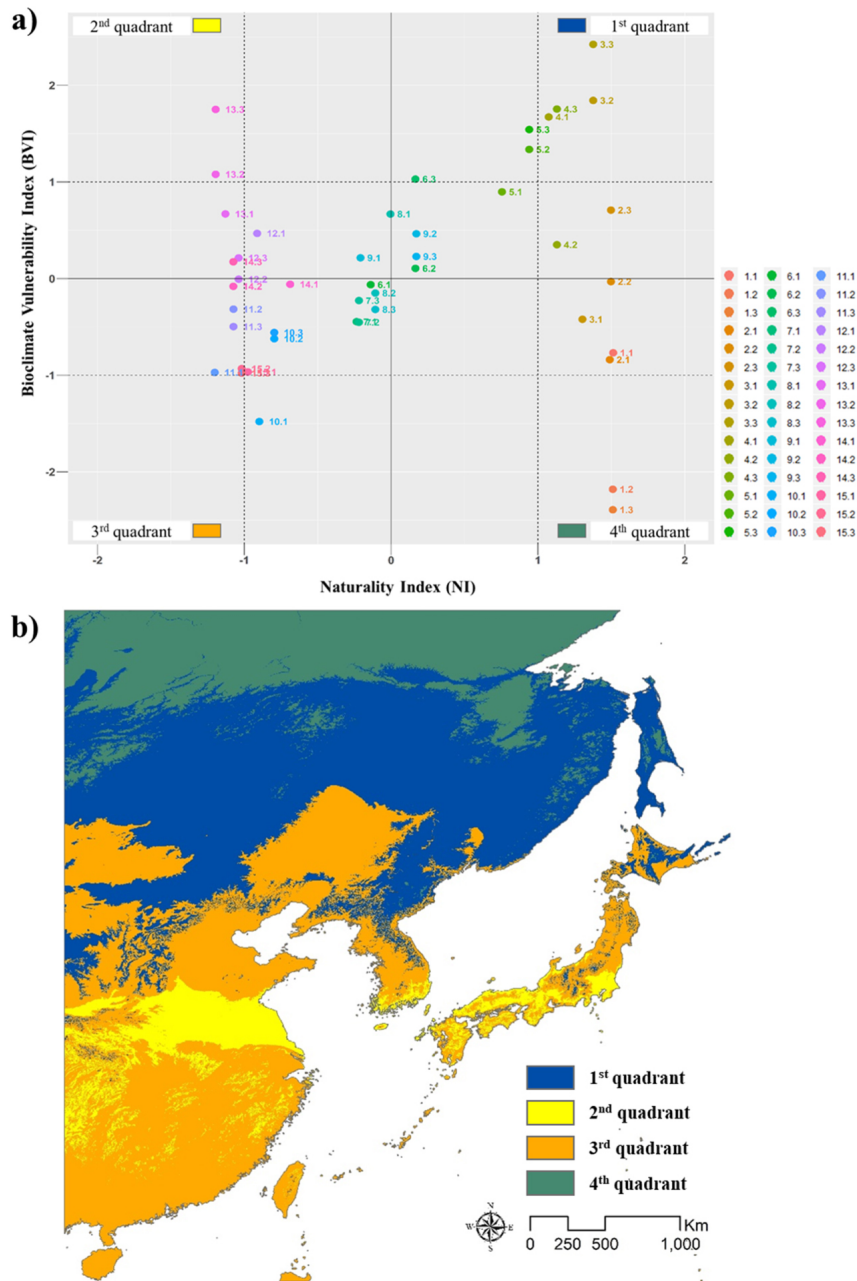


Figure 4: Results from the analysis in Choi et al. (2021) displaying a) the scoring of sites in North East Asia on the quadrant with the Naturality Index (NI) on the x-axis and the Bioclimate Vulnerability Index (BVI) on the y-axis. b) shows the spatial representation of each quadrant based on the calculated bioclimatic changes between the 2000s and 2050.

When used together in this manner, these indices have the potential to aid conservationists in identifying where novel ecosystems will occur due to anthropogenically induced climate and land use change. However, there are limitations to these metrics, including that the Biotic Vulnerability Index (BVI) uses equal weights for the changes in bioclimatic zone and moving speed. In reality, the weighting of these variables would

not be equal, rendering this index not completely representative of the system. Moreover, the Naturality Index (NI) utilises an assumption that land cover stays constant in the future, whereas this cannot be assumed to be the case. The authors recognise these limitations and attribute the latter to the lack of data availability for predictions on future land cover (Choi et al. 2019).

2.3 Biotic and Abiotic Indices' Use in the Literature

Despite the existence of such methods to quantify novel ecosystems as explored above, there is little evidence of their use in applied ecology. From searching the literature, there is no proof of the Biotic Novelty Index (BNI) (Schittko et al. 2020) being utilised except for its merging with the Human Novelty Index (HNI) to comprise the Urban Novelty Index (UNI) by Teixeira et al. (2021) (Figure 2). This is most likely due to the inclusion of the coexistence coefficient in the BNI calculation, which requires dates of introduction and residency time to be acquired for each species in the study community, a variable difficult to acquire. Even Teixeira et al. (2021) noted that there were no introduction dates available for the plants in their floristic surveys in the city of Porto, for which they were assessing urban novelty; ultimately resorting to estimating dates based on the rudimentary classification into “native”, “archaeophytes” and “neophytes”. Therefore, the attempt to quantify novelty based on the proportion of introduced species in the sample area is theoretically sound but empirically limited. Moreover, a high proportion of introduced species in a given site does not necessarily produce negative consequences for that site. Regardless of the results from the BNI and BNIs, further research is still necessary to understand the effects of novelty in that area to determine if any action is required.

There has been no evidence in the literature of the Urban Ecological Novelty Index (UNI) (Teixeira et al. 2021) being used to quantify novelty in urban contexts. Moreover, the UNI is not even referenced as a method to quantify novelty in an article with the same lead author regarding adaptive frameworks to mitigate urban planting under climate change (Teixeira et al. 2022), suggesting that the authors are not fully supportive of this methodology. One reason is perhaps due to the reliance on the Biotic Novelty Index (BNI) to place sites in the urban ecological novelty quadrant (Figure 2) for which the limitations in its calculation have already been discussed. This creates additional challenges for the researcher, as they need to calculate two distinct metrics, each relying on different variables, with the BNI requiring data that is often difficult to source.

The paper in which the standardised Euclidean distance (SED) formula was intro-

duced to measure abiotic novelty is well cited (176 times as of April 2025) and published in the reputable journal *Ecological Applications* (Radeloff et al. 2015). However, most of these papers only reference the importance of quantifying novel ecosystems and not the methodology itself. The lack of interest in this method is not surprising given that the R code has not been made available for reproduction, a likely hindrance to the SED formula's use in the applied ecology literature. Moreover, a potential limitation of this methodology is data availability. At a coarse scale, climate data is generally available; however, as Lugo et al. (2020) discovered during an attempt to calculate the SED for the tropical forests of Central and South America, a lack of high-resolution abiotic data for such areas impeded their ability to carry out this calculation as intended.

The second method analysed to quantify abiotic novelty: the Bioclimate Vulnerability Index (BVI), is also designed to represent results in a quadrant (Figure 4) with the Naturality Index (NI) on the x-axis and the Bioclimate Vulnerability Index (BVI) on the y-axis (Choi et al. 2019). Of the nine citations of this article, only one, authored by the same lead researcher, applied the BVI to confirm the maps created from various models of spatial trends in tree vitality (Choi et al. 2021). The BVI and NI offer indices with flexibility regarding their application across temporal and spatial contexts. The same methodology can be applied from local to global scale, offering insights into areas vulnerable to climate change for which suitable conservation strategies can be deployed, such as assisted migration (Higgs 2017; Hobbs et al. 2009; Kung 2023). However, the authors note that these metrics are not species-centric and will not allow for an understanding of how novel bioclimates are impacting species of concern (Choi et al. 2019). Nonetheless, this method can be used primarily to quantify past, current or future bioclimates in which further ecological surveying and monitoring should take place to identify vulnerable species.

3 Testing Existing Methodology

Of the aforementioned existing methods of quantifying novelty, the Biotic Novelty Index (BNI) (Schittko et al. 2020) and standardised Euclidean distance (SED) (Radeloff et al. 2015) were chosen for replication and further analysis. They were chosen over the Urban Ecological Novelty Index (UNI) and the Bioclimate Vulnerability Index (BVI) due to their higher citation rates and binary focus on abiotic and biotic factors. Also, the UNI is partially based upon the BNI; therefore, only one of these biotic metrics needs to be further analysed. A comparison of these metrics would be informative to a wider audience and to the understanding of the implications of quantifying novelty using different variables.

To begin, data sources were identified that would fit the requirements of these formulae. Those required for the BNI are species' coexistence dates and trait distances, and for the SED: human population, atmospheric nitrogen deposition, temperature and precipitation. The human population variable was excluded due to insufficient data availability for the required periods. Details of the methodology used to calculate each metric are provided below, with supplementary material for a deeper understanding available (see SM:3.1-3.2). All analyses were carried out with R version 4.2.3 (RCoreTeam 2023)

3.1 BNI Calculation

3.1.1 Obtaining and Cleaning the Data

To ensure that the analysis was based on a sufficiently rich, detailed, and curated dataset, UK birds were chosen to be the focal group due to the wide range of datasets available regarding their distribution, introduction times and functional traits (see Section 4 for a further application). Information regarding species distribution was taken from the breeding bird survey of the British Trust for Ornithology (BTO) (Gillings et al. 2019). Records are retained in Atlas periods across which sampling took place (1968–1972, 1988–1992 and 2008–11), allowing for a temporal trend of novelty, according to the Biotic Novelty Index (BNI), to be obtained. The Inventory of Alien Invasive Species in Europe (DAISIE) was used to obtain the introduction dates of birds (Roy et al. 2020), downloading data from the source archive. Traits were obtained from the AVONET, a widely used comprehensive database of functional traits for the global avifauna (Tobias et al. 2022).

A function in the R language was provided by the authors in the supplementary material to calculate the BNI, Rao's Q and BNIs (Schittko et al. 2020). This enabled an interpretation of how the datasets should be structured for this function to run successfully. The data from the BTO needed to be cleaned so all records were in a 10x10km grid cell resolution. Rare species of birds have recordings at 20km and 50km resolution, and bird species that have their location withheld are assigned a –10km resolution to protect their location (Gillings et al. 2019); thus, these species were removed from the analysis.

The traits chosen for this calculation were beak length (culmen), beak length (nares), beak width, beak depth, tarsus length, wing length, Kipps distance, wing width from the tip of the first secondary feather (secondary1), Hand-Wing index, tail length and body mass, retrieved from Tobias et al. (2022) chosen from the database to represent foraging strategy, locomotion and size.

To join the trait data to the distribution records from the BTO, some scientific names needed to be updated to the most recent taxonomy, checked against BirdLife DataZone (BirdLife International 2025) and the International Ornithological Congress (IOC) World Bird List taxonomic updates website (Gill et al. 2025). Furthermore, it was revealed that some species previously classified as two separate species have now been aggregated, for example, *Anthus spinolletta* and *Anthus petrosus* are now *Anthus spinolletta petrosus*. A total of 22 taxonomic updates were made, with the mean trait measurements of both original species calculated to form a single trait measurement for newly formed aggregates. Finally, vagrants were removed from the analysis because vagrant birds visit the UK rarely and temporarily and therefore contribute negligibly to the functional novelty of a site.

After data cleaning, separate data frames were formed with a list of unique species present in each Atlas period, with accompanying data frames containing the trait measurements for each of these species, separated by Atlas period (see SM:3.1.1).

3.1.2 Distance Matrix (`dist.mat`)

For each Atlas period, a distance matrix was curated by calculating the Euclidean distance between trait values. Euclidean distance was chosen as the morphological measures used are continuous. These distances can then be scaled using the maximum distance, following the code provided by the BNI authors (as tested in Section 2), by dividing each distance pair by its maximum distance. The distance matrices produced can now be substituted into the appropriate areas of the BNI function (see SM:3.1.2).

A histogram was used to visualise the distribution of trait values between species pairs across all three periods (Figure 5), displaying how the majority of species pairs have low Euclidean distance measures. This pattern is particularly evident in period 1 (1968–72), where there is a high rate of species pairs that have similar trait values. There are a few species pairs with larger trait dissimilarities recorded in period 1, but these are low in frequency. There are many fewer species pairs recorded in the second and third Atlas periods compared to the first (Time 2 and 3 in Figure 5); however, the distribution of trait distances is much more spread in these periods than in the first Atlas period. This is interesting considering that species richness is lower in period 1 than in periods 2 and 3 ($n = 220$, $n = 248$, $n = 248$, respectively). The temporal trend of species pairs' trait distances moves away from highly similar pairs and shows an increase in species pairs with more distinct trait values. This could reflect the prevalence of introduced species in the data during later periods.

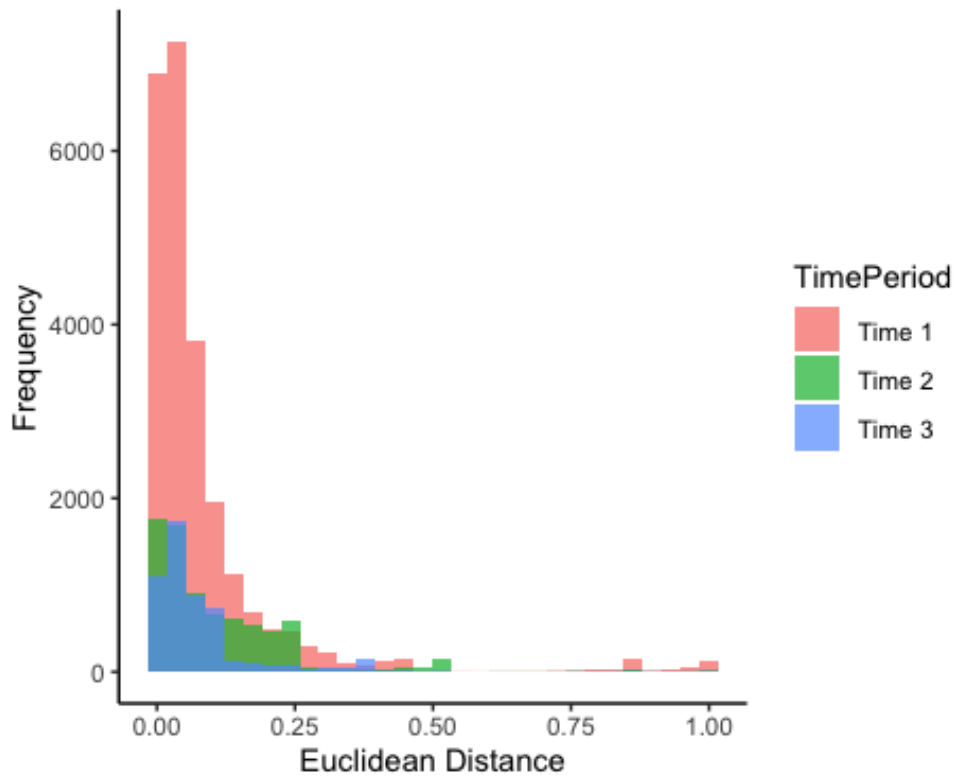


Figure 5: Histogram displaying the frequency of species pairs in each Euclidean distance category measuring trait dissimilarity. A high value of Euclidean distance indicates larger trait dissimilarity, whereas a lower value indicates trait similarity. Species pairs are organised into the Atlas period with Time 1 as 1968–72, Time 2 as 1988–91 and Time 3 as 2008–11.

3.1.3 Years Since Introduction (YSI)

Next, the first records of species occurrence need to be identified. Introduction dates were added to the species names using the dates downloaded from DAISIE. Species that were present in the BTO list but not in DAISIE were given an introduction date of 1492 and would be classed as ‘archaeobiota’ following the methods of Schittko et al. (2020), as they are native species. Each species’ status and introduction dates were verified against the BirdLife Datazone (BirdLife International 2025) and the GB Non-Native Species Secretariat website (Non-native Species Secretariat (NNS) 2025), and edited as required.

Once cleaned (see SM:3.1.3), these data frames can be substituted into the BNI function and converted into a coexistence matrix, which will be multiplied by the distance matrix.

3.1.4 Community Matrix (`com`)

Finally, a presence-absence matrix for each grid cell was developed. These consist of 1s and 0s depicting the presence and absence of each species per grid cell. Three of these matrices were produced, one per Atlas period (see SM:3.1.4).

3.1.5 Calculating BNI

Now the variables `dist.mat`, `trait.mat`, and `com` are ready to be employed within the downloaded code from the supplementary material provided by Schittko et al. (2020), using the R script entitled “gcb15140-sup-0003-Supinfo 3.R” which contained the BNI function. The variables will have three iterations to represent each Atlas period; consequently, the BNI function was run three times to get results for each period.

The calculation of relative abundance ($p_i p_j$ in the BNI formula, see Equation 2), which is an optional step according to the authors, was not included in this analysis, as the data used are based on presence-absence. Now the entire function can be run to produce BNI, Rao's Q and BNIs at each Atlas period (see SM:3.1.5).

3.1.6 Index Outputs

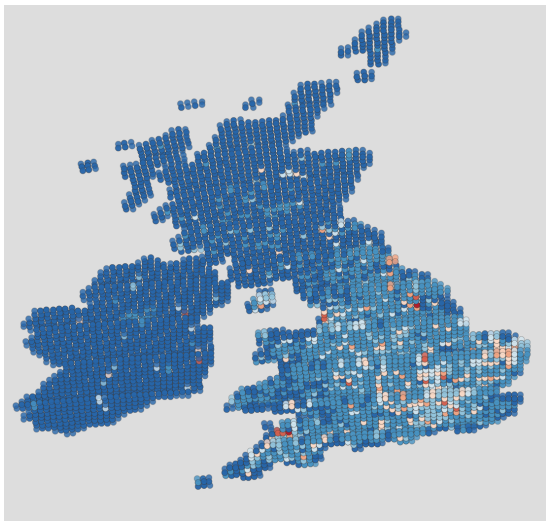
Three maps of BNIs at each Atlas period were produced (Figure 6) to illustrate the spatial and temporal trends of biotic novelty, as calculated by the BNI function. To identify the difference in BNIs value between Atlas periods, a box plot was produced showing the BNIs values across time (Figure 7).



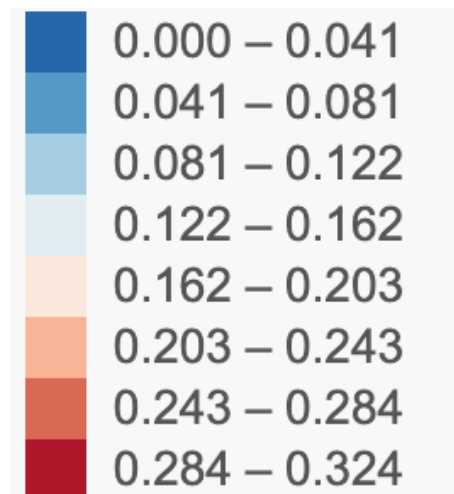
(a) 1968–72



(b) 1988–91



(c) 2008–11



(d) Scale bar of BNIs values

Figure 6: Maps of Great Britain and Ireland coloured by the standardised Biotic Novelty Index (BNIs) values in 10x10km grid cells according to the Ordnance Survey National Grid (OSGB) coordinates reference system. a) BNIs across the first Atlas period between 1968–72. b) BNIs in the second Atlas period of 1988–91. c) BNIs across the third Atlas period between 2008–11. The scale bar (d) shows values of BNIs indicating the minimum and maximum values across all periods.

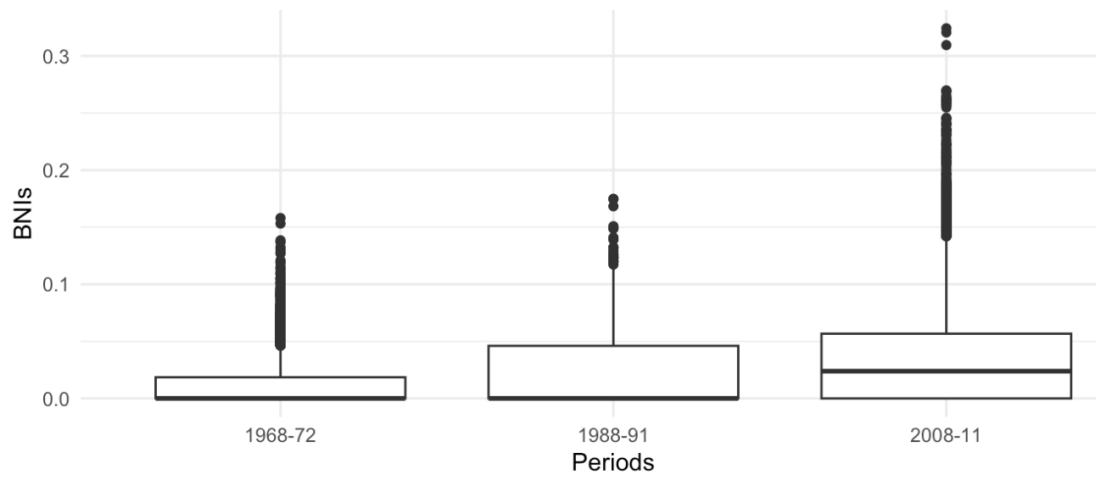


Figure 7: Box plot produced in R displaying the pattern in BNIs values. Note the small change in average values overall, but increasing range in values observed in the third Atlas period (2008–11).

3.2 SED Calculation

3.2.1 Obtaining and Cleaning the Data

The variables used by Radeloff et al. (2015) to quantify abiotic novelty were atmospheric nitrogen deposition, temperature, precipitation and human population. To ensure later comparison between the output of the BNI with that of the SED, data were required to span the same periods within which the BNI had been calculated. The Atlas periods range from 1968 to 2011, limiting data for the abiotic variables to this time frame. Unfortunately, no data are available for nitrogen deposition, temperature or precipitation in the UK that spanned this entire period. Therefore, we were limited to 1991–2011, reflecting the upper limits of the second and third BTO Atlas period. There was a lack of sufficiently spatially explicit data for the UK human population across these periods; thus, this variable was removed from the analysis.

Atmospheric nitrogen deposition in the UK was obtained from the UK Centre for Ecology and Hydrology (UK CEH) data archives (Tomlinson et al. 2021). This data contains wet and dry deposition of nitrogen and reduced (NH_x) and oxidised (NO_y) nitrogen. The total nitrogen deposition value was obtained by adding the columns for wet and dry deposition. Radeloff et al. (2015) did not specify whether reduced or oxidised nitrogen deposition was considered in their analysis. These are the two main forms of nitrogen, with NO_y emitted mostly from fossil fuel combustion and NH_x emitted primarily from agriculture (van den Berg et al. 2016). Therefore, reduced nitrogen deposition was chosen for this calculation because it represents land use change and can act as a proxy for human presence to compensate for removing the human population variable.

Mean air temperature and precipitation were taken from the Centre for Environmental Data Analysis (CEDA) archive in the HadUK-Grid gridded climate observations database (CEDA 2025; Hollis et al. 2019). Once the downloaded datasets had been read into R, maps and box plots were created for each variable at both periods to check the data before continuing onto the calculation to show the distribution of values (see SM:3.2.1).

To ensure results from the SED calculation were comparable to those from the BNI, the variables needed to be converted to OSGB grid cells and aggregated into 10km cells (see SM:3.2.1). All calculations were carried out with R version 4.2.3 (RCoreTeam 2023).

3.2.2 Creating a Function to Calculate SED

No code was provided by the authors of Radeloff et al. (2015); therefore, a function was developed to calculate the SED according to the formula (Equation 11).

$$SED_i = \sqrt{\sum_{k=1}^n \frac{(b_{ki} - a_{ki})^2}{s_{kt}^2}} \quad (11)$$

Equation 8 calculates the standardised Euclidean distance, developed by Radeloff et al. (2015), to measure abiotic novelty within the same grid cell at different time points. k is the index of the abiotic variables, $n = 3$ in this case, we are calculating SED with three abiotic variables. The term a_{ki} refers to the grid cell i at the baseline time point (a) with the value of variable k ; b_{ki} refers to the same grid cell but at the time point where novelty is being assessed. s_{kt}^2 represents the variance (S^2) of each variable (k) across all grid cells at the baseline time point (t) (Radeloff et al. 2015).

The steps involved in calculating this formula were to first calculate the variance of each variable at the baseline time (a). Then the result of $(b_{ki} - a_{ki})^2$ for each variable was divided by the variance for that variable. Next, all individual data frames for each variable were combined into one and summed by row to get one value per grid cell. Then, the square root of all values was calculated to get the SED value for each grid cell.

This function was tested to ensure it produced the expected output before using the empirical data (see SM:3.2.2).

3.2.3 Index Outputs

After calculating the SED, the results were merged with the longitude and latitude data for mapping using the mapview package to plot the results (v.11.2; Appelhans et al. 2023) (Figure 8).

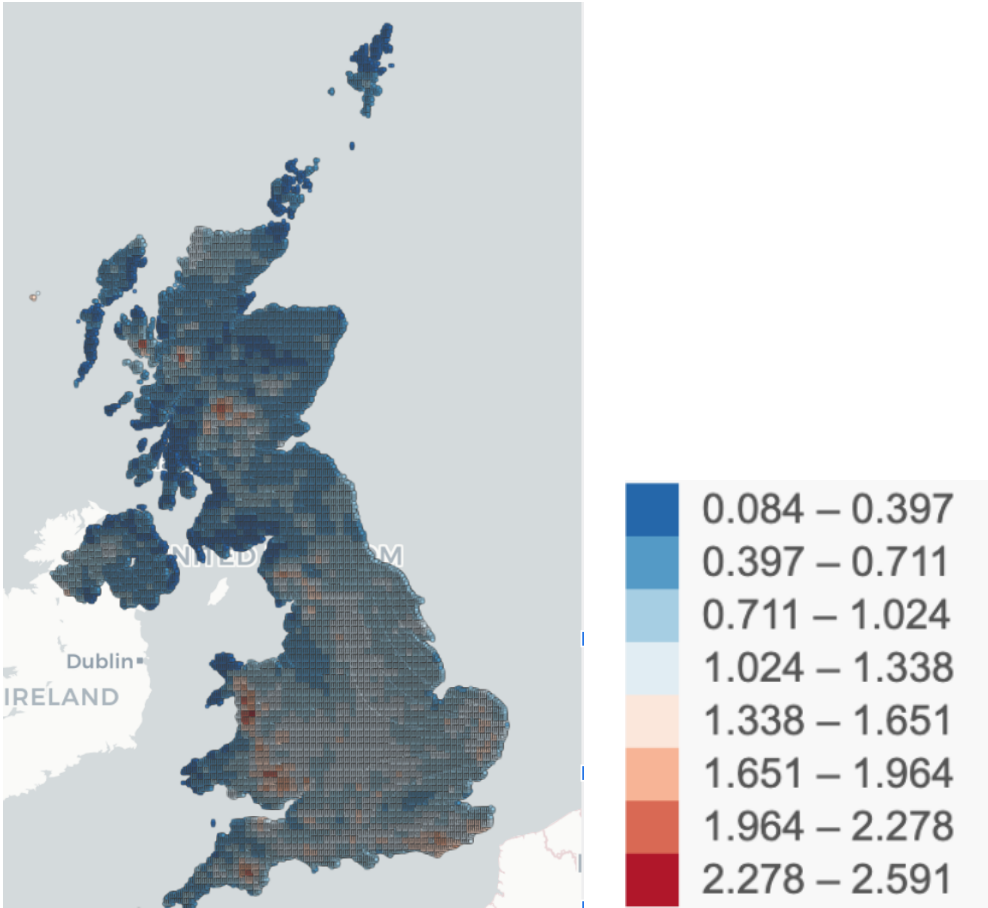


Figure 8: Map of novelty in the UK in 2011 according to the SED equation from Radeloff et al. (2015) coloured by values of SED provided by the scale bar. The novelty was calculated based on the variables of reduced nitrogen deposition, temperature and precipitation. Grid squares are in a 10x10km resolution with higher values of SED in red and lower values in blue.

To identify how each variable was influencing the overall SED value, the SED was calculated for each variable individually with maps to show the spatial distribution of values (Figure 9). The patterns of abiotic novelty in Figure 8 are undoubtedly a result of the combination of results shown in Figure 9. There are clear similarities between areas of high novelty highlighted by the map when nitrogen is the only variable included (Figure 9) and that of all variables in Figure 8, suggesting that the change in nitrogen was stronger between 1991 and 2011 than the change in other variables. To investigate this relationship further, a scatter plot was created to understand the correlation between the total SED values for all variables and the SED values when calculated for each variable (Figure 10). Here, the most notable correlation is between nitrogen deposition and the total SED values, confirming the previous visualisation.

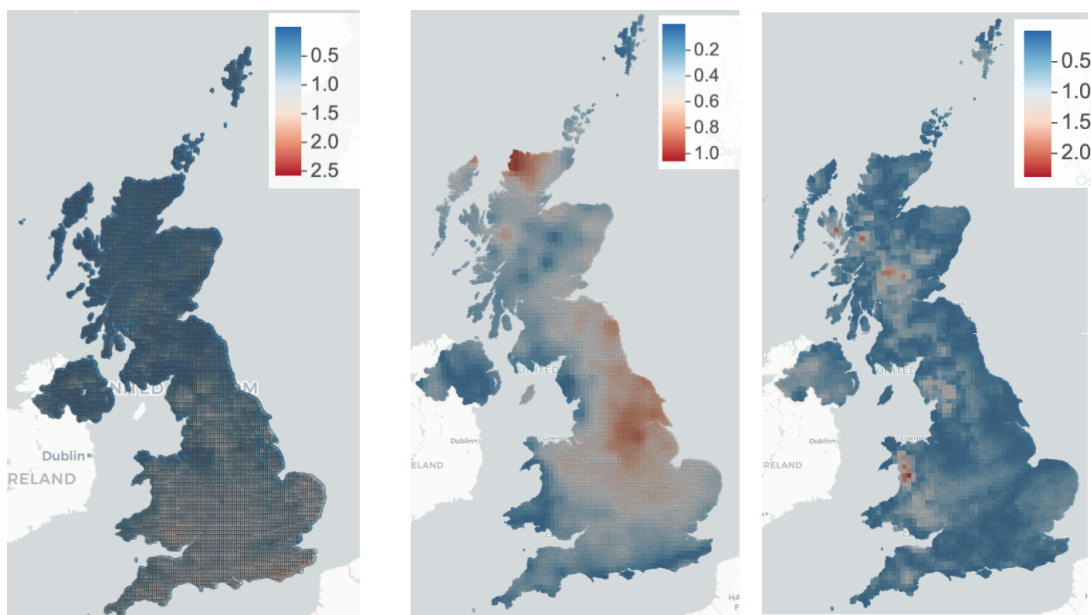


Figure 9: Three maps show the distribution of SED values calculated with individual abiotic variables across the UK. Left: map of SED values when nitrogen deposition is the only variable included. Middle: a map of SED values when temperature is the only variable included. Right: a map of SED values when precipitation is the only variable included.

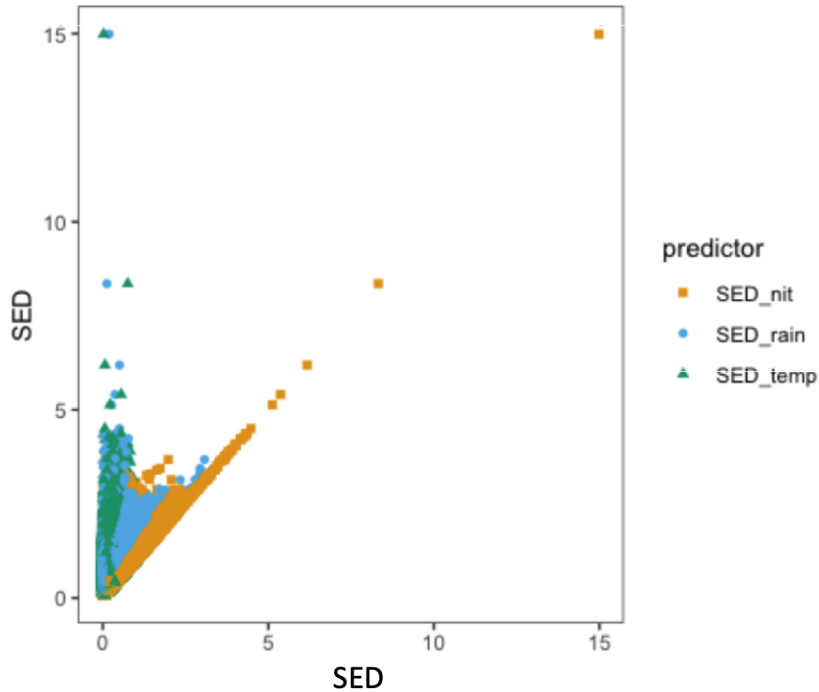


Figure 10: Scatter plot of SED values for each grid cell when all variables are included on the y-axis and SED values for each variable on the x-axis. The most prominent relationship is between nitrogen deposition and the total SED values of combined variables.

To identify any relationship between the values of novelty in grid cells calculated using the Biotic Novelty Index (BNI) and standardised Euclidean distance (SED), a scatter plot is provided with SED values on the x-axis and values of BNIs on the y-axis (Figure 11).

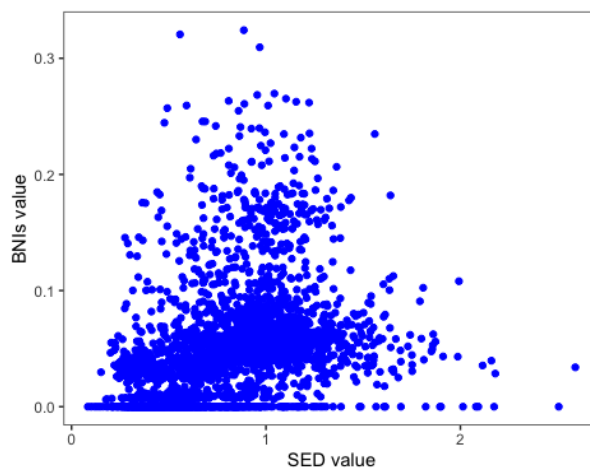


Figure 11: Scatter graph displaying the relationship between values of BNIs and SED.

3.3 Comparing the Results of the BNI and SED Methodologies

It is clear from the maps produced in Figures 6 and 8, and the scatter in Figure 11 that these two metrics offer different hotspots of novelty. The maps from the Biotic Novelty Index (BNI) calculation have hotspots of novelty around the South East of England, whereas the standardised Euclidean distance (SED) attributes high novelty in areas of Scotland and Wales (Figures 6 and 8). The significant differences in results from these two metrics were unsurprising, given the varied variables they include. Figure 11 further highlights the lack of a relationship between BNI and SED values in the same grid cell.

Biotic novelty is likely centred around the south of England due to the milder climates experienced here compared to the rest of the UK. This will allow invasive species from warmer climates to become established in the UK more easily (Pieck 2020; Kung 2023; Radeloff et al. 2015). This could also be due to the proximity of the south coast to Europe, allowing migrant birds to land here first from Europe. This is evidenced in the scatter plot coloured by latitude as higher values for BNIs are recorded at lower latitudes (see SM:3.3).

The correlation between the SED calculated for nitrogen deposition and the SED calculated with combined variables is interesting because the variables were normalised by their variance to ensure all variables are equally weighted. Therefore, it can be inferred that the years 1991 and 2011 must have a high dissimilarity in values for nitrogen deposition, causing the most variation in SED values across time. This is supported by box plots showing that the outliers have higher values of nitrogen deposition in 1991 compared to 2011 (see SM:3.2.1). Moreover, the hotspots of novelty indicated by the combined SED map (Figures 8) focus on upland areas including Snowdonia National Park, The Lake District and the Ben Nevis and Glen Coe Scenic Area. These are areas that likely receive high levels of rainfall due to their topography, influencing the higher SED values observed in these regions.

However, the SED only measures novelty compared to a baseline year, which creates issues regarding the reliability of the results. As observed in this analysis, nitrogen deposition was the most influential predictor of total SED values. However, this could be misleading as 1991 or 2011 could have been years that had exceptional levels of high or low nitrogen deposition. Therefore, incorporating a smoother method of measuring temporal variation in novelty within a metric would allow for comparison of novelty across time whilst accounting for high interannual variation.

The spatial differences in the results from the SED and BNI can be attributed to their focus on individual abiotic and biotic factors. This does not produce a holistic view of ecosystem novelty because it is well established that novel ecosystems are composed

of novel abiotic and biotic factors (Hobbs et al. 2014). It is inherent that individual taxa respond vastly differently to a change in abiotic variables. For example, bog and moor habitats were found to have increased fertility following increased nitrogen deposition, leading to a species composition change toward plants with a high nutrient affinity. In contrast, lowland heaths and grassland habitats decreased in fertility with increased nitrogen deposition (van den Berg et al. 2016). These findings show that an increase in a certain abiotic variable will have differing effects based on the habitat types in the study ecosystem. Measuring ecosystem novelty based on abiotic variables only does not comprehensively reflect the change in ecosystem function, as it is highly dependent on the species present within that ecosystem. Therefore, we suggest that a new methodology to quantify novelty contains both abiotic and biotic variables to represent ecological novelty comprehensively.

The BNI only allows one taxonomic group to be focused on at a time. In the paper, the authors focused on plant communities and in the present analysis, birds were the focal taxa (Schittko et al. 2020). This could be useful if there is a particular taxonomy that is of conservation concern and is threatened by novelty, such as trees in danger of climate displacement due to their slow range expansion (Ordonez et al. 2024). However, the BNI is not a feasible option for holistically representing the novelty within an ecosystem. If this were the goal, the BNI calculation could be repeated for multiple taxa and somehow merged, alongside a standardisation process, to create a more representative output. This requires much more time, effort and data collection, all of which I am certain stakeholders would struggle to ascertain. Therefore, a method that intrinsically involves multiple taxa without having to repeat the calculation would be preferred.

Moreover, using birds as a model taxa to calculate novelty does not reflect the transition of a novel ecosystem temporally. As birds are highly mobile, they will frequently be spotted in different grid cells than they previously occupied. Following the BNI, this will change the species composition and the subsequent set of functional traits in that area, leading to a different value of BNI. This reflects how the BNI is less informative on a larger scale, such as an entire nation, because it is based on the introduction of novel species, but it does not account for the movement of native species between the grid cells (as coexistence is defined at the full spatial extent of the dataset, in this case nationally). Consequently, metrics such as the BNI and SED can serve as an initial scoping tool to identify potential areas of novelty, but further investigation would be required at these sites to understand the impact of novel biotic and abiotic factors on that ecosystem.

As the authors portrayed in their case studies, the BNI could be more useful for

quantifying novelty in plant communities (Schittko et al. 2020), as they are immobile organisms compared to highly mobile birds. Plants are ecosystem engineers and often dictate which fauna exist in a given ecosystem (Kennedy et al. 2018). Therefore, studying novelty in plant species could be more representative of the ecosystem functioning compared to using birds. However, a multi-taxa approach would be preferred to quantify novelty in an ecosystem holistically.

One restriction to a multi-taxa approach with the BNI is the specific variables that it requires to be calculated. Trait (or phylogenetic) distance is needed for the taxonomic group of study to calculate the trait matrix. Databases containing such values are limited to well-studied groups of organisms such as macroinvertebrates, plants and birds (Tachet et al. 2010; Kattge et al. 2011; Tobias et al. 2022, respectively). Moreover, introduction dates of invasive species are not always well recorded for certain taxonomic groups, and this is a crucial element for the calculation of the BNI, which limits its applicability to different taxa and is a likely reason for its lack of uptake in the literature. Therefore, if the goal was to reproduce the BNI multiple times for each taxonomic group of interest to understand biotic novelty at multiple taxonomic levels, gathering the required data would be challenging and time-consuming. This results in a metric that is too complex for many stakeholders to use and understand.

In contrast, the SED offers more flexibility in the choice of variables, as it is possible to choose any variables that are of interest to the researcher. There is no limit on how many variables you can include, but the more you add, the more difficult it might become to identify the variable that is contributing the most to abiotic novelty. Despite this freedom in choice of variables, the SED makes calculation particularly challenging due to the lack of code available from the authors. There was no R script provided to calculate the formula, and neither were there descriptions of how the data needed to be formatted to reproduce the calculation. This led to a lot of time spent attempting to understand what the calculation required to work. This is time and effort that applied ecologists and stakeholders might not be willing to commit, and is likely a large reason why this method has not been implemented in the literature thus far.

Despite the authors of the BNI providing R code to calculate the formula and run their example case studies, it was challenging to understand the required format of the data. Their simulations did not provide example datasets on which to base this analysis; therefore, it was extremely time-consuming to get the data in the desired format. Moreover, depending on the data used, the BNI function, provided by the authors in the R script, needed to be edited. This step would be challenging for those not familiar with the R coding language, and even those with experience in coding struggled to understand how the function worked due to a lack of a detailed description.

Computationally, the metrics differ in their outputs. When standardised against Rao's Q, values of BNIs are bound between 0 and 1, which is useful when comparing sites across space and time. It is easy to interpret as the authors made it clear that a BNIs value of 0 indicates a community entirely of native species, whereas a value of 1 indicates a community entirely of invasive species (Schittko et al. 2020). In contrast, the SED has no upper bound, making the value difficult to interpret. It is only useful for direct comparisons between sites by indicating that one site is more or less novel than another. Thus, a new metric to quantify novelty should include a standardisation process, like the BNI, to ensure all values fall within a defined limit. This will also ensure that a standardised interpretation of the results can be made by all users.

When attributing values of novelty to a site, high spatial autocorrelation will most likely occur, especially when working on coarser spatial scales, such as 10x10km grid cells used in the present study. This can be a cause of error as neighbouring grid cells are likely to have similar values of novelty. However, the use of grid cells to quantify novelty may not be representative of the impacts on the ecosystem. Ecosystems are not bound within grid cells, nor are the biotic or abiotic variables used to measure novelty. Climate variables, including temperature, precipitation and atmospheric nitrogen deposition, will vary spatially but are not confined to particular ecosystems or study sites; neither are species of birds, as highly mobile organisms.

In conclusion, these metrics represent promising starting points for quantifying ecological novelty; however, there are several reasons why these methods should only be regarded as the foundation for developing a more comprehensive and representative approach to measuring novelty. Firstly, the focus on abiotic versus biotic variables causes distinct differences in the spatial distribution of novelty across the UK, failing to provide helpful advice to applied ecologists. More groundwork would need to be carried out to confirm the ecological novelty in that area. By definition, novel ecosystems are composed of novel abiotic and biotic factors (Hobbs et al. 2014); therefore, it is only natural that a method to quantify novelty combines these factors to present ecosystem novelty. Secondly, the BNI can only be calculated for one taxonomic group, which does not reflect the entire ecosystem's response to ecological novelty. Moreover, each abiotic variable used to measure novelty with the SED equation will have different effects on all organisms within that ecosystem. Therefore, neither of these approaches wholly represents the effect of novelty on the ecosystem.

Furthermore, the SED can only compare novelty with one baseline point, and you could only build up an understanding of the relationship of novelty through time by repeating the calculation for each year of interest, which would increase the data requirements and computational workload significantly. It is also deduced that a new

metric to quantify novelty should include a standardisation process, like the BNI, to ensure all values fall within a defined range. This will make it easier for all users to interpret the results.

Thus, it is concluded that these methods, the Biotic Novelty Index (BNI) (Schittko et al. 2020) and the standardised Euclidean distance (SED) (Radeloff et al. 2015), should be only used as an initial scoping mechanism to identify potential areas of novelty. They cannot be taken as a complete representation of ecological novelty, due to the arguments presented above, highlighting the need for a new method to quantify novelty.

Therefore, new methods were trialled in an attempt to fulfil the limitations explained above and provide a more comprehensive, reproducible and user-friendly method to quantify ecological novelty. Two metrics were explored, detailed below, using the same data sources as previous calculations described in this section.

4 Developing a New Method to Quantify Ecological Novelty

The main flaws of the BNI and SED that the above exploratory analyses identified were the separation of biotic and abiotic factors and the ease of reproduction. Therefore, the next goal was to develop a new method that combined both abiotic and biotic variables to get a total novelty score, using simple methodologies with basic data requirements, with interpretable outputs.

For consistency, the same variables used for the BNI and SED calculations were used here to allow for a direct comparison to the previously tested metrics. Later, a different data set, using macro-moths instead of birds, across a different temporal span, will be employed to show how this new concept can be successfully applied in multiple contexts.

4.1 Dissimilarity Metric

4.1.1 Methods

Firstly, a new method was trialled based on calculating the dissimilarity between variables at two time points; tested by calculating the absolute differences between abiotic and biotic variables separately and then combining them to get a total difference value. Species richness and trait distance were used as the biotic variables to offer an insight into ecosystem stability and functionality. Temperature and nitrogen deposition were taken as the abiotic variables to reflect land use change and climate change. Two variables for each biotic and abiotic measure are chosen so the results can be placed within a scatter plot, which is defined by a quadrant with each axis representing an individual variable or the total biotic or abiotic dissimilarity. This will allow for a visual representation of the results with easy interpretation for all users.

The data for trait distance was currently in a matrix format with numerous trait values per species. The mean pairwise trait distance for each grid cell was calculated by applying a function to the matrix of presences and absences created in the previous analysis (see SM:4.1.1).

As the abiotic data are limited to 1991 and 2011, the biotic data only from the second and third Atlas periods (1989–1991 and 2008–2011, respectively) were used, so all data are temporally aligned.

Values for mean pairwise trait distance and species richness for both Atlas periods were calculated and added to a data frame ready for the calculations to be carried out.

The calculations consisted of subtracting values from the second period from those in the third, followed by a scale and centre to bring all features to a similar range, so that each variable contributes more equally to the output. This process was repeated with the selected abiotic variables: nitrogen deposition and temperature (see SM:4.1.1).

To join abiotic and biotic results into one dissimilarity metric, the results for each variable were summed to get one abiotic value and one biotic value. These summed values could then be plotted on a scatter plot where each quadrant represents different directions of abiotic and biotic dissimilarity. These can subsequently be viewed spatially via a map of the British and Scottish Isles, using the OSGB coordinates in the downloaded BTO breeding bird survey data, taking inspiration from the quadrant output used by Choi et al. (2021). All analyses were carried out with R version 4.2.3 (RCoreTeam 2023).

4.1.2 Results

This method yields a dissimilarity value that can be plotted in a scatter graph, allowing for interpretation by quadrant position. Each quadrant represents the direction and magnitude of change in each variable (Figure 12a). From this, the results can be observed via a map of the British and Scottish Isles, denoting quadrant position by colour (Figure 12b). These results were then produced for the abiotic variables using the same methodology (Figure 13).

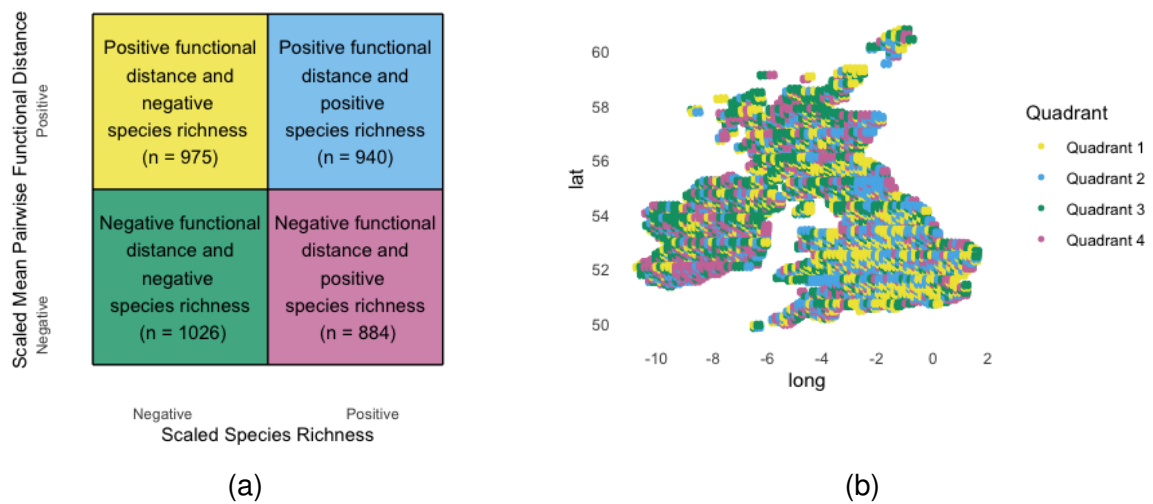


Figure 12: a) Quadrant schematic displaying how many grid cells are represented by different directions of biotic dissimilarity values. b) Map of the British and Scottish Isles coloured by each 10x10km grid cell's quadrant position on the scatter plot of biotic dissimilarity variables. Yellow represents quadrant 1, blue represents quadrant 2, green represents quadrant 3, and pink represents quadrant 4.

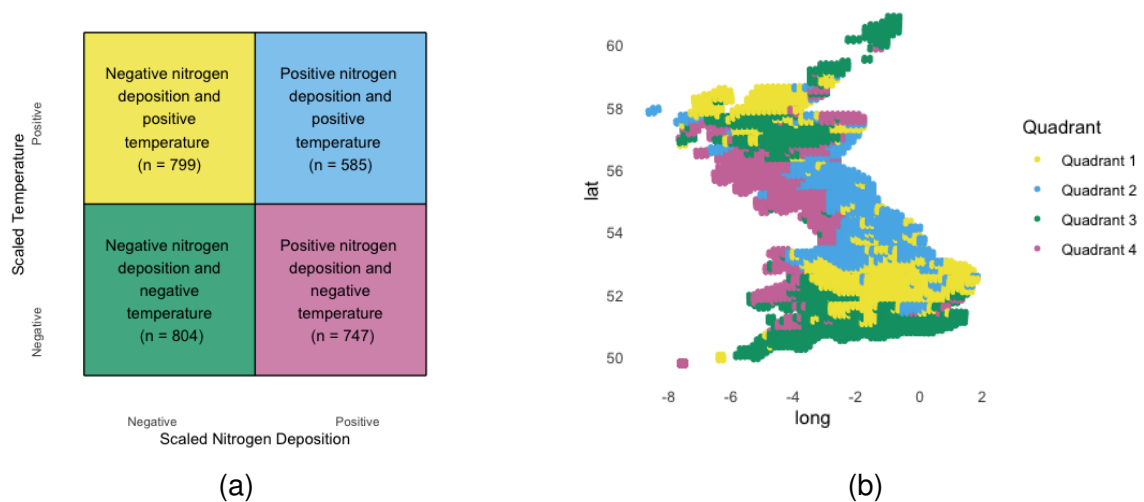


Figure 13: a) Quadrant schematic displaying how many grid cells are represented by different directions of abiotic dissimilarity values. b) Map of the British and Scottish Isles coloured by each 10x10km grid cell's quadrant position on the scatter plot of abiotic dissimilarity variables. Yellow represents quadrant 1, blue represents quadrant 2, green represents quadrant 3, and red represents quadrant 4.

With the summed values for each variable representing total abiotic dissimilarity and total biotic dissimilarity, another map was created to visualise the influence of factors producing novelty across the British and Scottish Isles (Figure 14).

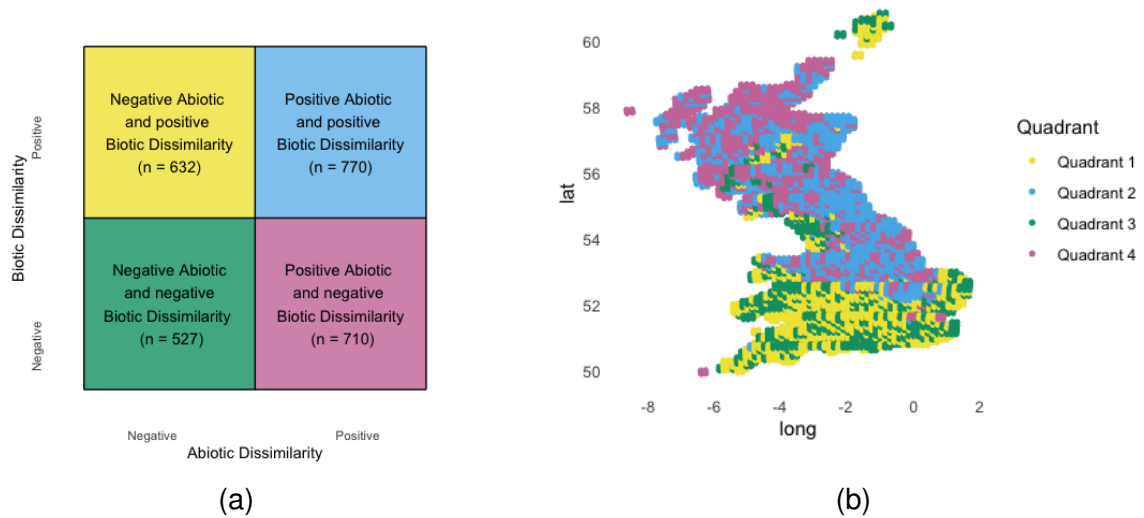


Figure 14: a) Quadrant schematic of how each grid cell is influenced by the summed abiotic and biotic dissimilarity values. b) Map of the British and Scottish Isles coloured by each 10x10km grid cell's quadrant position on the scatter plot of total dissimilarity calculated from the sum of the abiotic and biotic variables. Yellow represents quadrant 1, blue represents quadrant 2, green represents quadrant 3, and pink represents quadrant 4.

4.2 PCA Metric

4.2.1 Methods

After discovering the restrictions of the previous method defined in Section 4.1, which will be discussed in more detail below, a multivariate tool, such as a principal components analysis (PCA), offers a more accurate way to measure the distance between values at two time points without losing magnitude and directionality.

A PCA works by combining variables into principal components that can describe certain information about the dataset that has been used, creating orthogonal PC axes. The entire dataset is thus organised so that each principal component explains this information in order of representation and magnitude (Beattie et al. 2021). Therefore, the first principal component represents variables that explain the majority of the variance in the dataset, with decreasing representation as the principal components proceed.

A methods flow chart is used to summarise the methodology in Figure 15. To complete this method, two PCAs were performed, one for the biotic variables and another for the abiotic variables. Then, the dominant axes of both PCA results were combined to analyse the effects of abiotic versus biotic variables in driving spatial and temporal novelty in Great Britain. Unlike the previous dissimilarity method, PCAs require multiple variables; therefore, temperature, nitrogen deposition and precipitation were included for the PCA on abiotic variables.

Functional richness was calculated from the trait data downloaded from AVONET (Tobias et al. 2022) and the presence-absence data frame created via the BNI calculation as a third variable for the PCA on biotic variables. Functional richness was chosen over other diversity measures because it offers a way to understand the overall volume, in multidimensional trait space, that species in the study community take up (Mouillot et al. 2013). Therefore, functional richness offers an insightful way to compare how a community changes across time and space, calculated using `fd_fric` from the `fundiversity` package (Grenié et al. 2025).

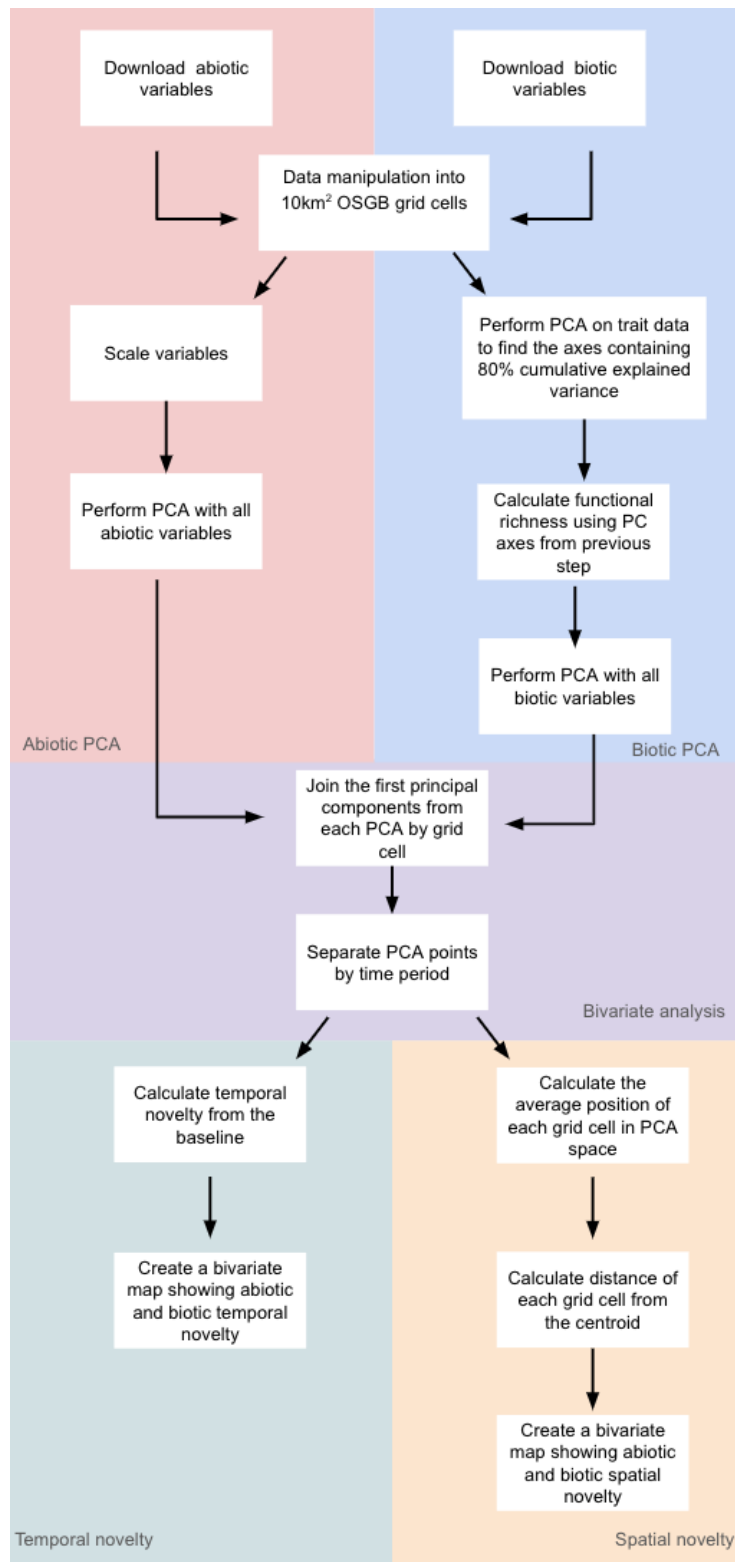


Figure 15: Flow chart to aid in the understanding of the PCA method to calculate temporal and spatial novelty using both abiotic and biotic variables.

We ran a PCA on the traits to produce trait axes and then selected the first three axes, which were calculated to contain 80% cumulative explained variance. We then used these principal components in place of the raw trait values for calculating functional richness, addressing the issue that morphological traits frequently display collinearity. This also makes the multidimensional geometry in the functional richness calculation manageable in a sensible time for the computer.

The variables for the PCA on biotic data consisted of functional richness, species richness and mean pairwise trait distance (calculated in the dissimilarity method in Section 4.1). The variables used in the PCA on abiotic data were temperature, nitrogen deposition and precipitation.

With the PCA results, Euclidean distance can then be calculated between the grid cell's position in PCA space at period 2 and its position at period 3 to get a measure of temporal dissimilarity. To measure spatial dissimilarity, the Euclidean distance can be calculated between a value of interest and the other grid cells in the same period, measuring how different each grid cell is in comparison to a certain value in that period. This was carried out by calculating the Euclidean distance to the centroid by identifying the average value for all grid cells.

These results can be visualised on a map of Great Britain by plotting the grid cells using the coordinates from the downloaded BTO breeding bird survey data (see SM:4.2.1).

To elevate this methodology and surpass the limitations of the BNI and SED, portraying biotic and abiotic impacts independently, the dominant axes of each PCA can be joined to identify the factors with the most influence over these trends, visualised with a bivariate map of Great Britain from the biscale package (Prener et al. 2022). This was carried out by selecting the first principal component axis (PC1) from each PCA on biotic and abiotic variables and employing the same methodology as above to calculate Euclidean distance as a proxy for spatial and temporal novelty. All analyses were carried out with R version 4.2.3 (RCoreTeam 2023).

4.2.2 Results

Euclidean distance was calculated between each grid cell at period 2 and its counterpart in period 3, to produce a map identifying grid cells with the largest Euclidean distance between time points, indicating higher temporal novelty. Individual abiotic and biotic maps of spatial and temporal novelty can be found in the Supplementary Material (see SM:4.2.2).

The temporal bivariate maps are to be interpreted as areas coloured blue indicating large biotic novelty across 1991 and 2011 and areas of red representing high abiotic

novelty, according to the Euclidean distances calculated from the PCA (Figure 16). The same interpretation applies to the map of spatial novelty from the average (Figure 17), as grid cells coloured red display large Euclidean distances in the abiotic variables from the centroid, and blue represents higher Euclidean distances in the biotic variables from the centroid. The colours decrease in intensity from red and blue, representing a scale of lowering Euclidean distances, with grey indicating extremely low values for both variables.

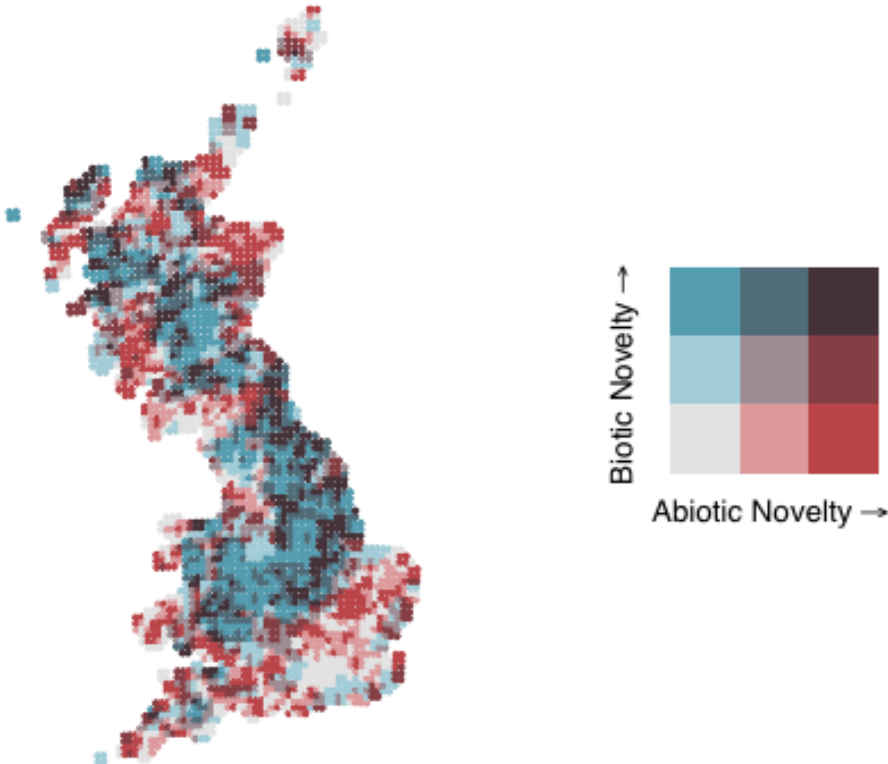


Figure 16: A bivariate map to display the temporal trends in abiotic and biotic variables indicated by the Euclidean distances between grid cells at the second and third Atlas period (1991-2011). The boldest coloured cells indicate those with larger abiotic and biotic novelty across this period, and those coloured pale grey represent grid cells displaying less novelty in both variables across this period.

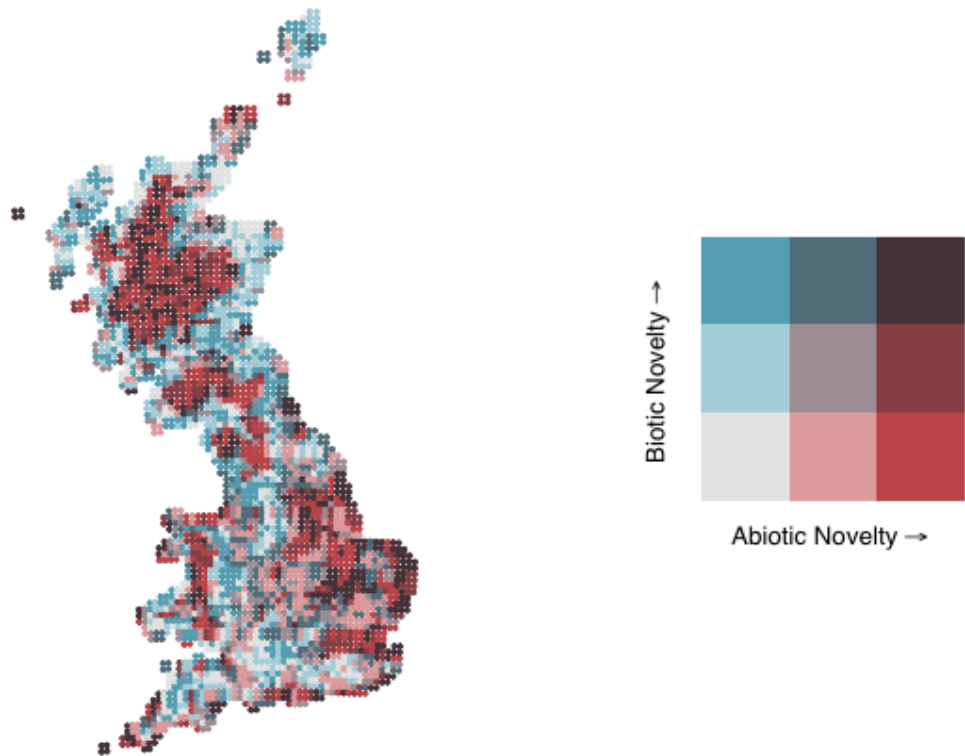


Figure 17: A bivariate map to display the spatial trends in abiotic and biotic variables indicated by the Euclidean distances to the average in the third Atlas period (2011). The boldest coloured cells represent larger Euclidean distances from the centroid, inferring high spatial novelty for that period. Paler coloured grid cells display shorter distances, inferring less spatial novelty from the average.

4.3 Discussion on New Methods

4.3.1 Dissimilarity Metric

The scatter plot of dissimilarity results from the biotic variables, species richness and mean pairwise functional distance, had the largest number of points in the third quadrant, containing grid cells with negative dissimilarity values for both variables (Figures 12a). This indicates that from 1991 to 2011, the years for which the data were collected, species richness and mean pairwise functional distance values decreased. Despite quadrant three having the largest number of points, the distribution of points throughout the scatter plot was fairly even, indicating that no overall trend of decreasing species richness or mean pairwise functional distance can be truly inferred.

When referring to the spatial distribution of grid cells and their quadrant position indicated by the biotic map of novelty (Figure 12b), Scotland, Ireland and areas around the English coast are dominated by green points, those in quadrant three, whereas the south of England and Wales are most obviously dominated by yellow and blue points, grid cells in quadrant one and two, respectively. Quadrant three contains grid cells with negative dissimilarity values for both variables, suggesting that in Scotland and Ireland, there were predominantly negative trends in species richness and mean pairwise functional richness. It is understood that seabird populations are under threat, particularly from overfishing, pollution and climate change (Bennett et al. 2025). Seabirds are noted as one of the two groups, along with upland birds, most threatened by climate change, as marine food webs are disrupted under rising sea temperatures and extreme weather events, causing adult mortality (Pearce-Higgins 2021). Therefore, it is likely that as the rate of global warming has increased to 0.36 °C per decade since 1980 (NOAA National Centers for Environmental Information 2025), this has negatively impacted bird species richness and subsequent functional distance across the UK shores, which could explain the pattern observed in Figure 12b.

The majority of inland grid cells in England and Wales are in quadrants one and two; from this, we can infer that in these areas, there is a positive trend for mean pairwise functional distance, but both positive and negative changes for species richness from 1991 to 2011. This suggests that perhaps the overall species richness isn't changing drastically in these areas, but the composition of species with a different subset of traits has changed in those grid cells. Bird distribution frequently varies per annum due to food availability, predator-prey dynamics and habitat preference (Wilson et al. 2002); therefore, it is highly likely that the bird community composition of a grid cell will differ when comparing two points in time. Nonetheless, a finer scale analysis, such as 1km² resolution, would be more sensitive to the factors determining bird distribution

and might have displayed more distinct patterns.

In contrast, the spatial distribution of grid cells correlated with their quadrant position when performing this method for the abiotic variables, temperature and nitrogen deposition, is much clearer (Figure 13b). Grid cells in quadrant one, displayed as yellow on the map, representing negative nitrogen deposition and positive temperature changes, are restricted to central England and North Wales. Those in quadrant two, depicted in blue on the map, represent grid cells that have experienced positive nitrogen deposition and temperature dissimilarities and are predominantly on the east coast of England, Wales and northernmost Scotland. Green points, grid cells in quadrant three that have shown negative nitrogen deposition and temperature change, are almost entirely clustered in the south of England and Wales. Finally, grid cells in quadrant four, represented by pink points, are distributed mainly along the West coast of Great Britain; these depict grid cells with positive nitrogen deposition dissimilarity but negative temperature dissimilarity.

The yellow regions on the map indicate that a temperature increase has occurred between 1991 and 2011; these areas contain major urban hotspots including London, Birmingham and Manchester. This observed increase in temperature in these areas coincides with a well-known symptom of climate change, the urban heat island effect, which causes cities to warm faster than rural areas (Heaviside et al. 2016). Therefore, these results are consistent with evidence for the urban heat island effect. However, it is interesting that the south coast of England is green, indicating a decrease in absolute nitrogen deposition and temperature values between 1991 and 2011. There are some interesting patterns arising here which would require a more in-depth analysis of this methodology. However, due to the dubious patterns suggesting that parts of the south of England are warming, whereas other parts are cooling, there is doubt in the accuracy of this method, due to the well-known trend of southern England warming faster than more northern areas (Kendon et al. 2024).

Regarding nitrogen deposition, reduced nitrogen (NH_x) was chosen for analysis over oxidised (NO_y) as it reflects agricultural intensity and is more directly linked to habitat loss and degradation. According to this methodology, reduced nitrogen deposition is said to have increased on the east coast of northern England and Scotland and to have reduced in the Midlands and the south of England (Figure 13b). In contrast, on a whole, reduced nitrogen deposition was recorded to have increased in the UK from 1990 to 2000 from 163 kt N to 211 kt N; with maps displaying the highest amounts of deposition to be focused in north west England, East Anglia and Devon in the year 2000 (Fowler et al. 2004). However, a more recent source says that from 1990 to 2017, reduced nitrogen deposition attributed to agriculture

has led to both increases and decreases across the country, with an overall trend for decreasing deposition (Tomlinson et al. 2021). Although neither of these sources clearly states how county-level trends in nitrogen deposition have changed over the past few decades, therefore, it is unlikely that the results from the dissimilarity metric can be verified without expert consultation.

The main benefit of this metric is its interpretability via the quadrant output, within which the results can be placed. This offers a way for non-ecologically trained stakeholders to immediately understand how the community of interest has been affected by the variable, or variables of interest.

Summing the dissimilarity scores for each variable together to produce total abiotic and biotic dissimilarity reduces the dimensionality of the original data. Such aggregation methods can lead to misleading results, as described in a particular case study within Anton et al. (2019), where the effects of invasive species on marine ecology were significantly underestimated due to the indiscriminate aggregation and averaging method employed by the original researchers. This can be particularly damaging when summing the results to assess impacts across opposing processes (such as nitrogen deposition and average temperature), as these are independent variables and have differing effects on the environment (Anton et al. 2019).

For the quadrant output to be applicable when analysing abiotic and biotic processes independently, only two variables can be viewed at a time, as one variable is needed per axis on the scatter graph. Therefore, this method limits the number of variables that can be included in a study to understand ecological novelty, a phenomenon that is famously complex and multifactorial. If multiple variables were to be studied using this technique, it would have to either be repeated multiple times per variable couplet, or a method of aggregation would be required to summarise the dissimilarity in the chosen data. In light of the issues of aggregation previously discussed, an inherently multivariate tool, such as a principal components analysis (PCA), offers a more suitable method to quantify ecological novelty whilst maintaining flexibility and reliability.

4.3.2 PCA Metric

The results from the temporal PCA metric on the biotic variables species richness, mean pairwise functional distance and functional richness, when represented in map form, don't display trends as clearly as the previous metric in Section 4.1.2 (see SM:4.2.2). Therefore, it is difficult to determine any regional trends in this map depicting temporal changes in biotic variables between 1991 and 2011. However, the maps depicting abiotic and biotic spatial novelty separately, via distance from the centroid,

offer some insights into the novelty of bird communities across Great Britain (see SM:4.2.2), which is also reflected in the bivariate maps.

The bivariate maps display to what extent biotic and abiotic variables are driving novelty, either temporally across 1991 to 2011 (Figure 16), or spatially, regarding the distance from the average novelty value (Figure 17). Interestingly, the map depicting temporal novelty displays areas of high biotic novelty, shown in blue on the map, to be restricted to inland England, Wales and areas of Scotland, suggesting that bird communities have changed the most in these areas. These biotic changes within the bird communities in these areas could be linked to the decrease of traditional crop rotations and mixed agricultural landscapes that have occurred since the late 20th century. Landscape-level changes such as these were predicted to have negative consequences for specialist farmland birds, as few species were recorded as generalists in one study assessing the impacts of farmland type on bird distribution patterns (Atkinson et al. 2002). A change in the resources provided by agriculture for birds would subsequently change their distribution, as specialist bird species relocate to find suitable resources.

In contrast, areas of high abiotic novelty, shown in red on the temporal bivariate map, are in the coastal regions of Great Britain and the Scottish Isles and the majority of East Anglia in England. This is supported by evidence stating that air temperatures for the UK near-coast records are, on average, warmer than records from the UK land between 1991 and 2020 (Kendon et al. 2024). Furthermore, the turn of the 21st century has brought the UK's wettest February, April, June, November and December on record (Kendon et al. 2024), affecting coastal regions more severely, highlighting the change in UK climate that is reflected in Figure 16. Of course, bird distributions are highly correlated to the climate; therefore, changes in the climate are linked to species distribution changes in altitude and latitude (Wilson et al. 2002). Despite this, the bivariate map of novelty shows areas of high biotic and abiotic novelty to be mostly segregated across Great Britain and the Scottish Isles.

There are evident hotspots of abiotic novelty around the Scottish Highlands, Lake District and East Anglia in England, indicated in red in Figure 17. Within these red zones are grid cells coloured by high abiotic and biotic novelty, the darkest shade on the colour scale, suggesting that regions with significant abiotic changes are where high biotic novelty is observed. This pattern is expected as bird distribution is highly influenced by weather and the climate (Wilson et al. 2002). Moreover, it is also shown in this map that there is high novelty occurring along the coast, with this pattern most evident along the south coast of England (Figure 17). This observation is consistent with the previous discussion, indicating that the coastline has been more significantly

affected by severe weather events (Kendon et al. 2024).

From this analysis, it could be viewed that the bird community has shifted its distribution toward areas with lower abiotic novelty. This change is attributed to the stability in these regions, as both bivariate maps indicate that high biotic novelty is present outside the red areas, which are characterised by high abiotic novelty. An inconsistency between the two maps is the indication of high novelty along the coastlines in Figure 17, contrasted with the absence of this pattern in Figure 16. It was noted in a study that undertook the same methodology as the British Trust for Ornithology's (BTO) Breeding Bird Survey, that seabirds were under-recorded (Wilson et al. 2002), suggesting that data used for this analysis also suffered from low representation of seabirds. This recorder bias could explain the difference in patterns of novelty occurring across the British coastline when viewed temporally versus spatially.

The bivariate visualisation of this method is effective at easily identifying the key drivers of novelty in areas of interest, allowing for further investigation to be employed if required. It is highly recommended that the outcome of Euclidean distance calculations be represented in this form due to the ease of comprehension.

A multivariate tool, such as a principal component analysis (PCA), means this method is flexible to the researcher's interest. This method works with a minimum of three variables, which will be valuable to those working in under-recorded areas where data is limited. Moreover, different combinations of variables can be tested to explore different research questions, providing a reliable and reproducible tool for researchers. As an ordination method, data is summarised in a lower-dimensional space; therefore, the patterns and relationships between variables in the data can be recognised more easily when represented in PCA space. Ordination analyses also reliably transform data whilst keeping the magnitude and direction of the variance in the data due to the underlying use of Euclidean distances in a PCA (Beattie et al. 2021). Regardless of this method's benefits, the temporal analysis is currently limited to comparing two time points, which, as previously discussed, can produce misleading results. To reiterate, if one of the years used to measure abiotic temporal novelty was a particularly wet, hot or high nitrogen deposition year, this will skew the results and will not reflect the general trend in these variables across study periods. The same is true for bird distributions, as migrations and nesting success are dependent on numerous variables, and thus can vary highly from year to year (Camp et al. 2023). Recorder effort also needs to be taken into account as a possible cause of error when using data collected by numerous people across the country, such as that from the BTO's breeding bird survey. However, a different way of applying this methodology could be to measure the average distance to each year in a defined base period. This wasn't investigated in the current study,

although it would be interesting to compare our results to this different approach.

One of the drawbacks to this method is that it requires some previous statistical knowledge and skill for its implementation. This includes the computational effort needed to perform a PCA on statistical software such as R (RCoreTeam 2023), whereas the calculations required to measure dissimilarity between points could be carried out in Microsoft Excel and only require minimal statistical knowledge. Furthermore, a comprehensive understanding and interpretation of the outputs of a principal components analysis (PCA) does require existing knowledge of its inner workings. Therefore, it is recommended that this method be primarily employed by researchers in the ecological field. Although with the detailed descriptions of the methodology and interpretation of results provided (see SM:4.2), this metric should also be useful to individuals from a broader background, such as land managers and conservation planners.

The next step for this metric will be to employ the same methodology using different data. Ideally, using different variables across a new geographic location and taxa, to demonstrate how this method is applicable and flexible to multiple contexts. Therefore, new abiotic and biotic variables from different taxa across a different temporal scale will be identified for the suitable reproduction of this PCA method.

4.4 Putting the New PCA Method into Practice

Following the same methodology as above (Figure 15), the PCA method was employed with different datasets, focusing on macro moth distribution across Britain and the Scottish Isles between 1970 to 2018 (GBIF 2025). Traits were obtained from Cook et al. (2022). The abiotic variables were changed to maximum and minimum temperature, average sunshine hours and precipitation, gathered from the same online resource that was previously used, from the Centre for Environmental Data Analysis (CEDA) (CEDA 2025; Hollis et al. 2019).

The variables were converted to 10x10km OSGB grid cells, averaging the values to aggregate the data to a common scale, which will be used as the abiotic variables for the PCA. Using the trait and distribution datasets, functional richness, diversity, evenness and dispersion were calculated using the package *fundiversity* (Grenié et al. 2025) to act as the biotic variables for the PCA. With this, a PCA was performed on the scaled abiotic and biotic variables separately, and the first axes of each were selected for creating the bivariate maps.

Temporal abiotic and biotic novelty was found by separating the PCA results by year (1970 and 2018) and calculating the Euclidean distance between each grid cell in PCA space at the different times. This was then plotted using the *biscale* package (Prener et al. 2022) to display the influence of abiotic and biotic variables explaining novelty between 1970 and 2018.

For measuring spatial novelty across this region, an average value was taken from the first principal component axes of the abiotic and biotic PCA to be used as the target value. Using this, the Euclidean distance from the centroid could be calculated to get a measure of novelty compared to the average. This was then plotted as a bivariate map to show the influence of abiotic and biotic variables on inducing spatial novelty in 2018.

4.4.1 Discussion of Results

The aim was to employ the newly developed PCA method in a wholly different scenario, with new taxa, geographic location and abiotic variables. However, it was discovered to be highly demanding to find data with these requirements that were compatible with this calculation. Therefore, limited by the overall time constraint of this project, the same dataset was used to collect abiotic variables, but the variables themselves varied from previous analyses (CEDA 2025; Hollis et al. 2019). This meant constraining this analysis to Great Britain. As a well-recorded species in this location, macro moths were chosen as a new taxon to work with for this analysis, as distribution and trait data are readily available (e.g. GBIF 2025; Cook et al. 2022). However, the new taxa and

temporal scale still reflect the reproducibility of this method and its potential adaptability to new contexts, provided the data are available.

The bivariate map depicting temporal novelty from 1970 to 2018 shows high abiotic novelty to be primarily focused along the east of England, with areas going through the middle of Scotland and into the Scottish Isles (Figure 18). This matches trends depicted from recent State of the UK Climate reports, showing areas of the south east of England to have the highest count of days per year at the maximum temperature for the UK. Moreover, half of the UK’s ten wettest years have been recorded since the 21st Century (Kendon et al. 2024). This contributes to the high abiotic novelty shown by the map, in which precipitation was a variable, in Figure 18.

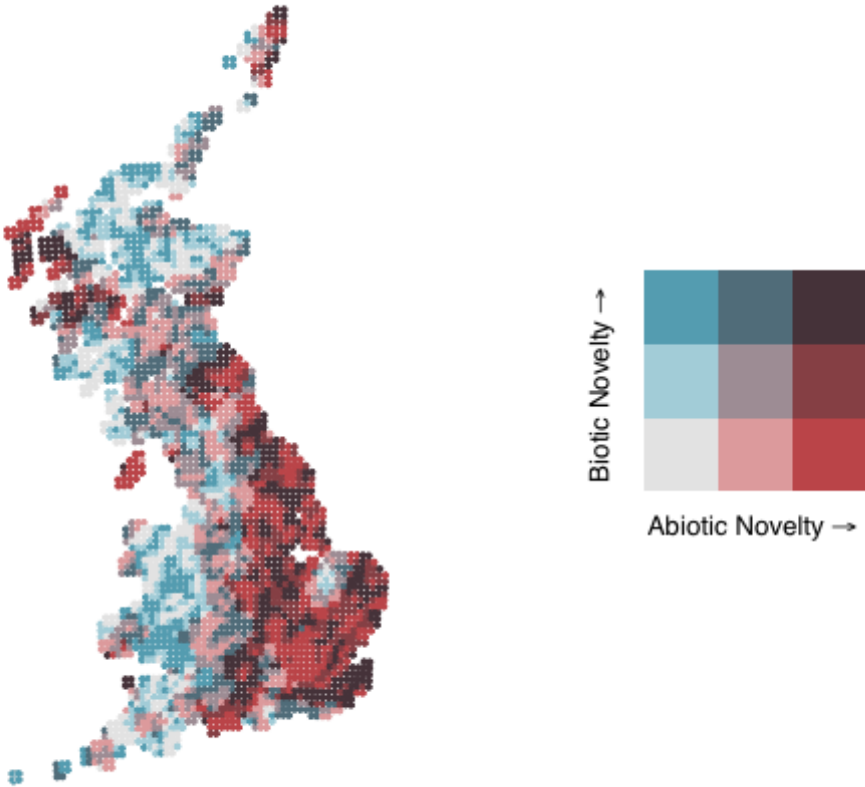


Figure 18: Bivariate map showing the Euclidean distances calculated from the abiotic and biotic PCA across 1970 and 2018. Variables used for the abiotic PCA were maximum and minimum temperature, sunshine hours and precipitation. Variables used for the biotic PCA were moth functional richness, diversity, evenness and dispersion. Note the difference in patterns observed here compared to Figure 16.

In contrast, biotic novelty is focused on the west side of England and the majority of Wales, suggesting that functional measures of macro moths have changed here,

despite a lack of change in abiotic variables. This is slightly contradictory when examining evidence from Butterfly Conservation, which states that macro moth losses were higher in the south of Britain compared to the North between 1968 and 2017 (Fox et al. 2021). However, there is no evident pattern in biotic novelty from Figure 18; therefore, we can infer that moth distribution has changed rather uniformly across this geographic region from 1970 to 2018. This is supported by the State of Britain's Larger Moths 2021 report which found that 32% of species saw a distribution decrease whereas 37% saw an increase in distribution (with the remaining 31% witnessing no significant trend in distribution change) (Fox et al. 2021); explaining why there is such patchy biotic novelty observed across Figure 18. Furthermore, as many species of macro moths are habitat specialists due to the reliance on host plant availability for larval growth, this inconsistent trend in biotic novelty is reflected in the findings from the report that woodland and open grassland breeding moths increased in distribution whereas moorland breeding moths decreased in distribution, evidencing how habitat availability is an importance factor for macro moth persistence. Further changes in moth distribution could be witnessed over this century as climate risk assessments predict that over 60% of the 422 moth species assessed could experience an increase in distribution due to climate change, adding that range expansion is often limited by habitat availability (Fox et al. 2021).

Regarding the temporal trends in moth distribution, these are likely skewed by the 48 year-long distance between the two points assessed. When downloading the distribution data from the Global Biodiversity Information Facility (GBIF) (GBIF 2025), there was a reasonable difference in records in 1970 compared to 2018 (199,085 versus 1,741,369, respectively). This indicates an increase in recorder effort in more recent surveys, which would lead to biased results. Thus, any observable pattern in moth distribution may stem from the underrepresentation of moths in the records from 1970. Unfortunately, this is often the issue when working with long-term datasets such as these.

In the bivariate map of spatial novelty from the centroid in 2018, high abiotic novelty is clustered around the south coast of England, coastal Wales and patches of mainland Scotland (Figure 19). This suggests that the abiotic variables used for this analysis, maximum and minimum temperature, sunshine hours and precipitation, are vastly different in these areas compared to the average. This pattern is unsurprising as the highlighted areas are mostly coastal, which have markedly distinct weather regimes compared to inland areas. 2018 was a particularly cold year for the UK, with significant snowfall experienced from February to March that year. During this time, maximum temperatures were up to 10 °C lower than the seasonal average (Greening et al. 2019),

causing large dissimilarity in the minimum and maximum temperature variables used for the abiotic PCA. This would provide one explanation for the high abiotic novelty portrayed along upland and coastal areas of Great Britain and the Scottish Isles in Figure 19, as these areas generally experience lower temperatures (Greening et al. 2019). Also, supporting evidence from the Met Office shows long-term trends in southern districts of the UK warming more compared to other regions (Prior et al. 2014), which is reflected in the red areas focused along the south coast in Figure 19.

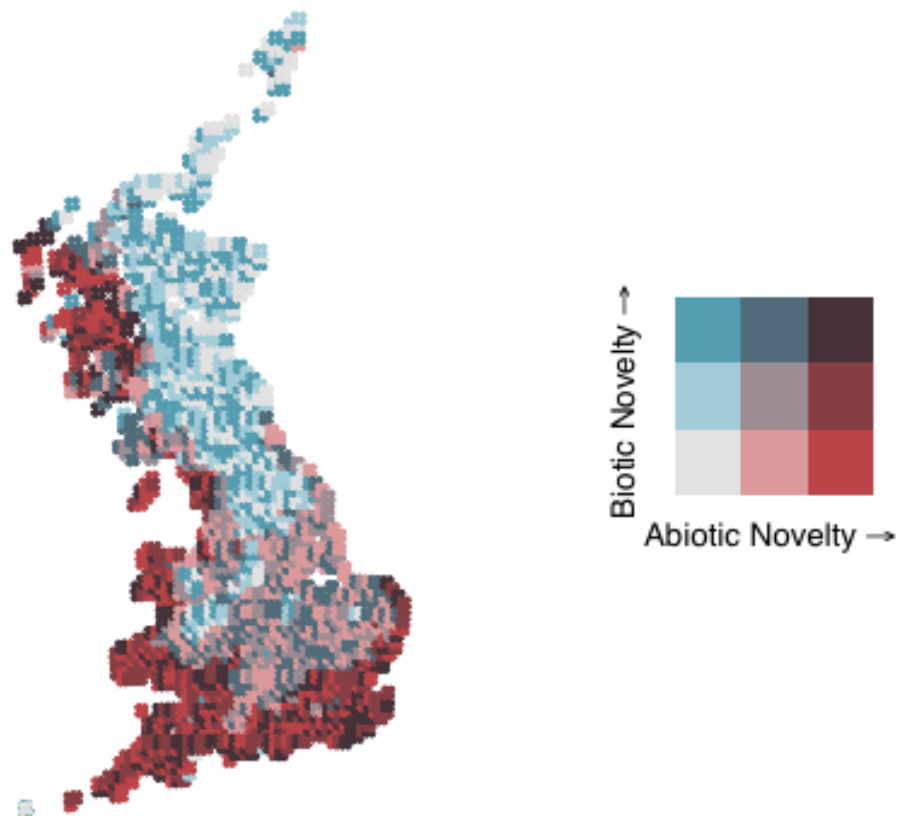


Figure 19: Bivariate map of novelty depicted by the Euclidean distances calculated from the average of all points in the PCA axes. Note the stark differences in novelty hotspots here compared to those in Figure 18.

Patches of biotic novelty are spread across the majority of the region, with no clear pattern indicating how moth distributions differ from the centroid. This is highly likely because many species of macro moths are habitat specialists, suggesting why there aren't many obvious patches of high biotic novelty, because the functional community is constrained to habitat type.

Supporting studies show that numerous moth species, including habitat general-

ists, specialists and colonists, are becoming more common due to anthropogenically induced change, as moth distributions are becoming increasingly homogenised. Such drivers of these trends are hypothesised to include increasing expenditure on conservation, habitat change providing novel opportunities and climate change creating favourable conditions (Boyes et al. 2019). Although it is worrying that areas of high moth species richness, according to the status of macro-moths of Great Britain report (Fox et al. 2021), overlap with areas of high abiotic novelty indicated by Figure 19. This suggests that these areas could contain moth species at risk from climate change.

It is also vital to note that, due to this method being an ordination analysis, it is not possible to compare this to, for example, global novelty, as the results are dependent on the spatial extent of the data fed into the principal components analysis (PCA). Moreover, if one wanted to infer novelty in one section of the map, Wales, for example, it would not be comprehensive to just ignore the rest of the points, as the values of novelty are calculated from the entire dataset comprising England, the Scottish Isles and Wales. Therefore, it is recommended that, if a separate analysis was requested for just one area, the whole calculation would need to be conducted with data for that area alone.

5 Conclusion

Under the influence of the Anthropocene, ecosystems are pushed over tipping points, leading to novel abiotic and biotic conditions. These novel ecosystems will continue to prevail under ongoing environmental change, highlighting the urgency to understand the effects, both positive and negative, of novelty.

An enhanced understanding would improve conservation efforts under novel conditions, influencing the adaptation and evolution of new methods and management practices. First, we need a measurable way to assess novelty in ecosystems to develop context-specific strategies. As evidenced by the literature review, such a measure does not currently exist without its flaws and lack of popularity within the scientific community.

The Biotic Novelty Index (BNI) and standardised Euclidean distance (SED) were tested in this research project to identify key advantages and disadvantages of these existing methods that can be taken forward in the development of a new method to quantify ecological novelty (Schittko et al. 2020; Radeloff et al. 2015, respectively).

Such disadvantages, and likely reasons for their limited uptake, include how they focus on biotic and abiotic novelty separately, despite the most commonly used definition of novel ecosystems stating they comprise both novel abiotic and biotic conditions (Hobbs et al. 2014). Moreover, the BNI methodology is highly restrictive towards data requirements, proving hardship in sourcing reliable data to put into the formula. However, one advantage of the SED method is that the variables included are interchangeable, meaning each researcher can adapt the methodology to their research interests. This aspect in particular was taken forward into the development of a new method to quantify novelty.

Firstly, a method based on calculating the difference between variables at two time points was trialled, by first calculating the difference between biotic and abiotic variables separately, and then summing those results to get a total dissimilarity measure.

The advantage of this method is the output's interpretability via the quadrants and adjoining maps. This allows stakeholders with non-scientific backgrounds to understand the general trend in novelty and to understand if abiotic or biotic factors are having the most impact on novelty in certain areas. A major disadvantage, however, is that the total novelty is based on summing the dissimilarity scores; this reduces the dimensionality of the original data, causing potentially misleading results that do not reflect the underlying variance of the data.

To overcome this issue, a multidimensional metric was sought, leading to the development of a principal components analysis (PCA) based methodology. This metric involved carrying out a PCA for the biotic and abiotic variables of choice

individually, and then joining the first principal component from each PCA to show the influence of each factor contributing to novelty across the study area. The key benefit of this new methodology is that it is an ordination analysis, meaning the patterns and relationships of the data are reflected in lower-dimensional space. Furthermore, as with the dissimilarity method, it is flexible as to which variables are put into the PCA, provided there are at least three variables and that they are not collinear. Examples have been shown with two taxonomic groups, birds and macro moths, demonstrating this methodology's flexibility to different research requirements. One drawback of the PCA method is that it is still limited to comparing two points in time, which can create misleading results, as one year could have been anomalous. This is an issue which needs to be considered when interpreting results and will require further research into how best to adapt this method for more reliable outputs.

This PCA metric is presented as an ongoing piece of research, to stimulate conversations on how to quantify novelty in the most accurate, reproducible and accessible way. We encourage an interdisciplinary approach to allow for the production of creative and exciting ideas on how to quantify ecological novelty. Collaboration is necessary to address the ongoing challenges and opportunities faced by the Anthropocene.

Abbreviations

BNI	Biotic Novelty Index
BNIs	Biotic Novelty Index standardised against Rao's Q
BTO	British Trust for Ornithology
BVI	Bioclimate Vulnerability Index
CEDA	Centre for Environmental Data Analysis
DAISIE	The Inventory of Alien Invasive Species in Europe
GBIF	Global Biodiversity Information Facility
HNI	Human Agency Novelty Index
IOC	International Ornithological Congress
NI	Naturality Index
NHx	reduced nitrogen
NNSS	Non-native Species Secretariat
NOAA	National Oceanic and Atmospheric Administration
NOy	oxidised nitrogen
OSGB	Ordnance Survey National Grid
PCA	Principal Components Analysis
Rao's Q	Rao's Quadratic Entropy
SED	Standardised Euclidean Distance
SM	Supplementary Material
UK	United Kingdom
UK CEH	United Kingdom Centre for Ecology and Hydrology
UNI	Urban Ecological Novelty Index

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