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# Dark diversity dynamics linked to global change: taxonomic and functional perspective

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# Dark diversity dynamics linked to global change: taxonomic and functional perspective

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Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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# LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, mentioned in the text by Roman numerals:

I. **Trindade D.P.F.**, Carmona C.P., Pärtel M. (2020) Temporal lags in observed and dark diversity in the Anthropocene. Global Change Biology 26, 3193–3201.

II. **Trindade D.P.F.**, Carmona C.P., Reitalu T. & Pärtel M. (2023) Observed and dark diversity dynamics over millennial time scales: fast-life history traits linked to expansion lags of plants in northern Europe. Proceedings of the Royal Society B: Biological Sciences 290, 20221904

III. **Trindade D.P.F.**, Pärtel M., Carmona C.P., Randlane T. & Nascimbene J. (2021) Integrating dark diversity and functional traits to enhance nature conservation of epiphytic lichens: a case study from Northern Italy. Biodiversity and Conservation 30, 2565–2579.

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Author's contribution to the publications:

I. Developed the idea, led the manuscript writing.

II. Developed the idea, analysed the data, led the manuscript writing.

III. Participated in the development of the idea, analysed the data, led the manuscript writing.

# 1 INTRODUCTION

## 1.1 Background

Global changes (e.g. climate and land-use change) are imposing important threats to biodiversity and, consequently, to human well-being. Over the few last millennia, humans have accelerated climate warming and land-use change, driving species' extinctions and redistributing biodiversity worldwide (Mottl *et al.*, 2021). Global changes have the potential to reshuffle biodiversity because they modify important filters that affect how communities are assembled across spatial and temporal scales (Urban *et al.*, 2012; Pecl *et al.*, 2017). Thus, examining how global changes affect the way species disperse, cope with environmental conditions and interact locally is then essential to quantify and forecast biodiversity change. For example, according to the community assembly theory, a local site includes a subset of the species in the region that are able to colonize and establish locally, which usually depends on the functional traits of these species – measurable characteristics of an individual organism (Götzenberger *et al.*, 2012; Zobel, 2016). During the community assembly process, some species in the region are not able to cope with the local environmental conditions (i.e. environmental filtering), making them unsuitable to the local site's condition. Some other species display certain functional traits that enable them to cope with those environmental conditions but also the biotic filter (i.e. competition, predation etc.), successfully colonizing and establishing locally (observed diversity). Finally, there is a set of species that are theoretically able to overcome the environmental filtering, being locally suitable, but are absent (dark diversity) (Pärtel, Szava-Kovats and Zobel, 2011) (Figure 1). Both observed and dark diversity compose the site-specific species pool. Identifying these species enables us to calculate how complete or realized each local site is, allowing for diversity comparisons in a relative way (community completeness index, which is the ratio of observed to dark diversity) (Pärtel, Szava-Kovats and Zobel, 2013). By depicting the set of locally absent species that are ecologically suitable and present in the surrounding region, dark diversity provides an operational link between regional and local scales (Pärtel, Bennett and Zobel, 2016). Thus, dark diversity may reveal species going locally extinct as well as species in the region becoming locally suitable after global change, being a useful tool to track biodiversity change across space and over time. However, after the onset of a global change driver, species in observed and dark diversity might respond with some delay, since species usually take some time in going locally extinct after an environmental change (extinction debt) or in colonizing a new suitable local site (expansion lag) (Kuussaari *et al.*, 2009; Alexander *et al.*, 2018). Although the dark diversity concept had been used to explain how local communities are assembled across scales, prior to this thesis no studies had directly examined the effects of global changes on both observed and dark diversity across space and over time.

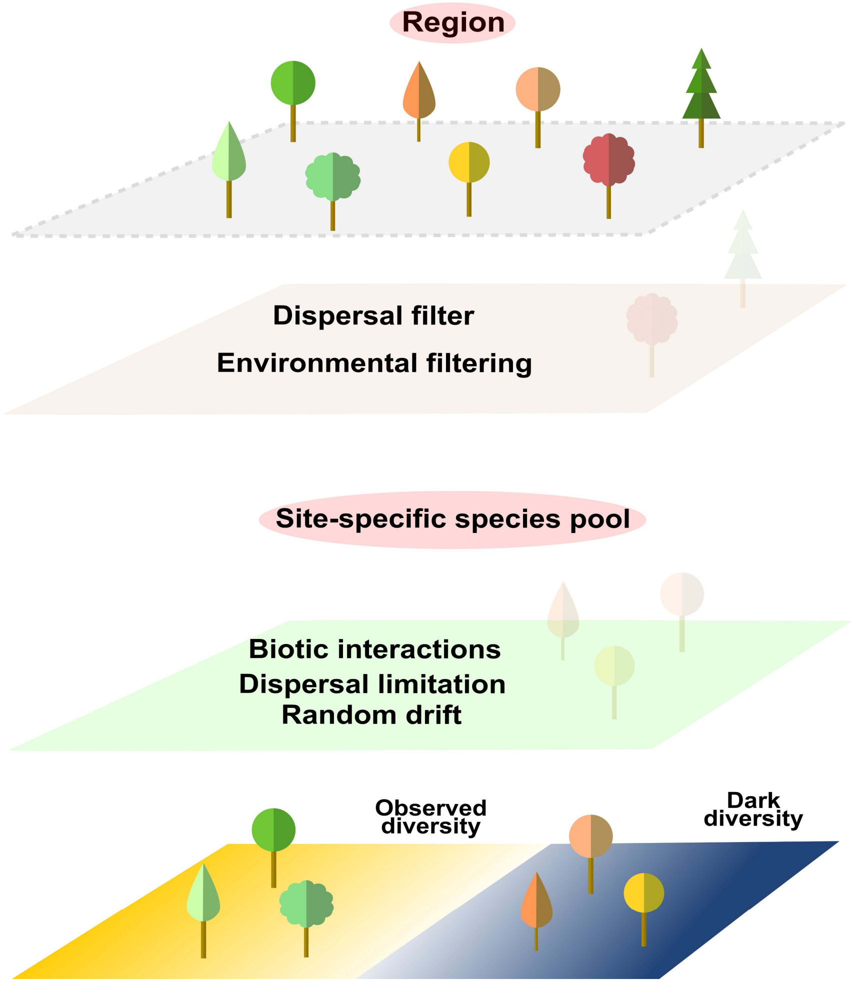

**Figure 1**. Conceptual figure depicting, how the community assembly process occurs from regional to local scales. Species in the region (top grey quadrat) need to overcome different filters (i.e. environmental and large scale dispersal) in order to establish locally. Some species are present in the region but cannot overcome the first filters (dispersal and environmental filters), thereby they are not suitable to the local sites' condition (faded species in the brown quadrat). Species that can overcome those filters are considered part of the site-specific species pool. In order to establish locally, these species still need to overcome some other local filters (i.e. biotic interactions and stochastic processes; green quadrat). Some of those species have successfully established locally (species in the yellow quadrat), whereas other species, despite being potentially able to colonize and establish locally, are absent, comprising the dark diversity of that local site (species in the dark blue quadrat).

Comparing the functional traits in observed and dark diversity helps explaining how the filtering process works from regional to local scales, revealing which traits are favoured and which traits are hampered. For example, species with traits related to lower dispersal capacity and stress intolerance are often part of dark diversity (Riibak *et al.*, 2015). In addition, plant species that depend on strict mutualistic associations may also become part of dark diversity when their mutualists are lacking (Moeslund *et al.*, 2017). Considering individual traits, however, overlooks the fact that plant responses depend on the whole phenotype. A more holistic way to understand how traits determine which species are observed and which ones are in the dark diversity of a site is to analyse traits in combination (Carmona *et al.*, 2016). This approach informs us about what parts of the functional space (i.e. a space based on traits) are occupied by observed species (observed functional diversity) and what parts are occupied by species in dark diversity (Carmona *et al.*, 2016). Although the concepts of functional space and observed functional diversity are already well established in ecology, the idea of 'functional dark diversity' started to be empirically tested more recently, helping to disentangle the effect of different filters during the community assembly process (i.e. dispersal and biotic filters) (Belinchón, Hemrová and Münzbergová, 2020; Morel *et al.*, 2021). In this thesis, I aim to clarify this concept and provide different examples of how it can be applied. Since, by definition, dark diversity is the set of species suitable but locally absent, here I propose the functional dark diversity as the portion of functional space that could be theoretically locally occupied but is absent. In this way, species in taxonomic dark diversity occupying the same functional space of species already present locally (functional observed diversity) do not contribute to the functional dark diversity but are functionally redundant instead. Such a functional redundancy between observed and dark diversity could be an indication of higher stability and resilience of the local communities. For instance, since the species in dark diversity are playing a similar functional role as the species locally present in other sites of the surrounding region, being potentially able to buffer functional local losses (Rosenfeld, 2002; Biggs *et al.*, 2020; Auber *et al.*, 2022).

Those losses or gains of species and traits in the species pool will likely occur with temporal lags (Kuussaari *et al.*, 2009). In order to examine species pool dynamics and temporal lags, long-term datasets are required. Palaeoecological data is a reliable way to reconstruct millennial time scale biodiversity dynamics, providing important insights on how biodiversity might change in the future. For example, fossil records have been used to reconstruct mammal and bird niches over the last millions of years, revealing groups that were mostly affected by global changes and might be affected in the future (i.e. large-bodied animals with low dispersal ability and slow pace of life) (Smith *et al.*, 2022; Germain *et al.*, 2023). For plants, sedimentary pollen data is currently the most common source of information on how vegetation dynamics have changed in the past (Reitalu *et al.*, 2015; Reitalu *et al.*, 2019; Nogué *et al.*, 2021). Recent studies suggest that both climate and human impact were crucial to shape the biodiversity of plants over the last 15,000 years at the global scale, with human impacts accelerating biodiversity change more recently (ca. 2,000 years BP) (Mottl *et al.*, 2021; Nogué *et al.*, 2021). These changes affected the filtering processes mentioned above, both at the taxonomic and functional levels. For example, after the Late Glacial period new species and traits became suitable, enabling the expansion of the functional space (Reitalu *et al.*, 2015). During the Holocene, different climatic fluctuations and human activities shaped the taxonomic and functional diversity of plants (Blonder *et al.*, 2015). Human activities became more pronounced in Europe during the Late Holocene, increasing habitat heterogeneity and decreasing the dispersal limitation of several taxa, but also suppressing some taxa and functional groups (i.e. taller and large seeded plants) (Reitalu *et al.*, 2015). For instance, before the onset of agriculture, taller and large seeded plants thrived in Europe and North America, mostly due to animal dispersal (Knight *et al.*, 2019; Butterfield *et al.*, 2019). However, after the beginning and intensification of agricultural practices, taxa displaying resource-acquisitive traits were mostly favoured (i.e. herbaceous, ruderal and pastoral taxa) (Reitalu *et al.*, 2015; Veeken *et al.*, 2022). It is likely that dark diversity dynamics can inform species that became unsuitable, as well as those that persisted in dark diversity of potential sites, indicating an expansion lag in taxa's geographic range, prior and after these important climatic and human impact events. For example, in a scenario of increasing observed and dark diversity size but taxa presenting expansion lags, the community completeness is expected to decrease over time, indicating that although the species pool size is increasing, more species persist in dark diversity.

Apart from temporal assessment, global change effects on biodiversity can also be examined using space-for-time substitution, in which contemporary spatial data is used to infer temporal processes, having important implications for nature conservation (Blois *et al.*, 2013). Historically, ecologists have been using such approach to examine how species change along environmental gradients, being an important source of theories and concepts in ecology (e.g. secondary succession and water-energy dynamics) (Clements, 1916; Gleason, 1917; Hawkins *et al.*, 2003). Those environmental gradients can be used as a proxy of global changes effects on biodiversity in the near future. In that sense, mountains are considered an important open laboratory to examine, for example, how climate affects biodiversity, since climatic conditions can change rapidly, sometimes in relative short distances, along elevational gradients (Körner, 2007; Rumpf *et al.*, 2018). Examining dark diversity and functional traits in such a context can provide novel pathways to enhance both conservation and restoration activities. For instance, functional traits can be compared in observed and dark diversity revealing either threatened functional groups that may disappear or species and functional groups that are locally suitable and could be restored (Lewis *et al.*, 2017). Whether a site should be restored or conserved can be theoretically assessed from the community completeness index. For example, it is suggested that when the community completeness index is low (i.e. more species in dark diversity compared to observed), more attention should be given to restoration practices, since there are relatively more species available and suitable in the region than locally realized (Lewis *et al.*, 2017; Noreika, Pärtel and Öckinger, 2020). Thus, those species are expected to be facing some delay in their colonization or establishment (Török and Helm, 2017). On the other hand, if the community completeness is high (i.e. more species in observed diversity compared to dark diversity), it is suggested that more conservation efforts are needed, since there are not so many suitable species able to buffer potential local losses (Lewis *et al.*, 2017).

Species with narrow climatic niches, such as lichens, are more sensitive to climate warming and are considered a good model to infer global change effects because they tend to respond rapidly to those changes (Nascimbene and Marini, 2015). Different studies have shown that lichen diversity decreases under warmer conditions, and some traits related to thallus growth form, photobiont type, and reproduction strategy confer either higher resistance or likelihood to extinction (Nascimbene and Marini, 2015). For example, crustose lichen species (growth form type) are considered more tolerant to drought, whereas macrolichens (i.e. foliose and fruticose growth forms) are less tolerant (Larson, 1981). The dispersal of lichens can also be assessed from their reproduction strategies, with sexual species usually having higher dispersal abilities over asexual species (Yahr, Vilgalys and DePriest, 2006; Morando *et al.*, 2019). However, lichens reproducing sexually depend on the availability of a suitable photobiont at the settled location to establish, whereas asexual species have usually heavier diaspores dispersing closer while they do not depend on such association (Tehler, 1982; Belinchón, Yahr and Ellis, 2015). Thus, if species with low dispersal ability are those more often found in dark diversity, restoration activities can focus in assisting the dispersal of those species. However, if the proportion of species reproducing sexually is higher in dark diversity, the focus of restoration should be on decreasing the establishment limitation. Therefore, examining both observed and dark diversity, as well as community completeness, and functional traits of lichens may enhance our ability to predict how both species and traits in observed and dark diversity are changing, providing a nature conservation guideline at the species pool level.

## 1.2 Objectives of the thesis

The main aim of this thesis was to examine the role of dark diversity as a relatively novel and complementary tool to assess and quantify biodiversity change across space and time.

The specific aims of this thesis were:

1: To explore how efficiently dark diversity can be used to decompose biodiversity change. With observed and dark diversity one can decompose biodiversity change in two space-related components: one associated with local gains and losses and another related to gains and losses of site-specific species pool. Those gains and losses will depend on whether global changes lead the environment towards more benign or harsh conditions. Taxonomic and functional observed and dark diversity are expected to increase (local and pool gains) towards more benign conditions due to less stringent environmental filters and higher diversity of available niches (**I**, **II**, **III**).

2: To identify possible temporal lags in biodiversity change using dark diversity. Over time, dark diversity is expected to depict species in expansion lags, because species appearing and persisting in dark diversity are considered suitable despite being absent for long periods of time. Such an expansion lag may happen when the creation of new niches outpaces the ability of species to colonize and establish locally. In such a scenario dark diversity will increase faster than observed diversity, decreasing community completeness over time, since more species are becoming part of dark diversity, but they are not realizing locally (**I**, **II**).

3: To use functional traits to understand why species are in dark diversity and, when examined over time, in expansion lag. Traits related to low dispersal ability and high stress intolerance are expected to be found more often in dark diversity, and, thereby associated to species with delays in local colonization or establishment (**II**, **III**).

4: To enhance nature conservation by integrating dark diversity, community completeness and functional traits. Dark diversity reveals species and traits threatened by regional extinction or that could be focused on restoration efforts. Community completeness provides insights on whether a site should be restored (low community completeness) or conserved (high completeness) (**I**, **III**).

# 2 METHODS

## 2.1 Study area and vegetation

To examine effect of global changes on observed and dark diversity dynamics, I used different approaches, locations and organisms. Paper **I** was a conceptual work, thereby no empirical data was used. In paper **II**, to test the effect of climate warming and human impact on observed and dark diversity dynamics, I used a sedimentary pollen data collected in 20 sites in northern Europe, from Reitalu *et al.* (2015). The study area is located between the boreal and nemoral forest zones, consisting mostly of *Picea abies*, *Betula pendula*, *Populus tremula* and *Pinus sylvestris*. This region has experienced important changes in both climate and human impacts over millennial time scales, with marked effects on vegetation dynamics (Figure 2 – upper panel).

In paper **III**, to test the effect of climate on dark diversity in space and its consequences to nature conservation, I used a lichen dataset along an altitudinal gradient in Italy, from Nascimbene and Marini (2015). The study was carried out in North Italy, in the alpine region of South Tyrol where mean annual temperature ranges between 11–12°C in the bottom of the main valley (Adige valley) and 2–3 °C above 1700 m a.s.l. Spruce forests dominate the landscape between 900 and 1900 m a.s.l. representing 52% of the total forest cover. These forests are mainly managed with progressive thinning and exploitation of mature trees.

## 2.2 Estimating Dark Diversity

Dark diversity cannot be directly observed, only estimated. Different methods are currently available to estimate dark diversity size in each local site (see a mini review in paper **I**). Among the available methods, those that rely on the co-occurrence between species are considered the most accurate. They are based on the notion that species that co-occur more often tend to share similar ecological requirements. I can illustrate this idea with a very simple example: consider a focal species, which tends to frequently co-occur with another species. If the focal species is absent from a local site but the other species that frequently co-occurs with it is present, it is likely that the focal species is part of the dark diversity of that site. Two different co-occurrence methods were used in this thesis (Hypergeometric in paper **II** and Beals Index in paper **III**). Both Hypergeometric and Beals methods use the realised number of co-occurrences between pairs of species to estimate which species are in dark diversity (Lewis, Szava-Kovats and Pärtel, 2016; Carmona and Pärtel, 2020). Accordingly, this information was used to construct a taxa × taxa indication matrix reflecting the strength with which each species co-occur with all other species. Using this indication matrix, the algorithm calculates the mean indication for all absent taxa, using present taxa as indicators. This way, I can assign to all taxa absent from a given site a probabilistic estimation that they belong to the dark diversity of the site. In the

Hypergeometric method, the probability for any given focal taxon is high if the present taxa are generally positively associated with the focal taxon (i.e. if it tends to co-occur more than expected by chance with the present taxa) (Carmona and Pärtel, 2020). The probabilities predicted by the Beals index are usually correlated with the frequency of the species in the dataset (**III**), which can be corrected by applying species-specific probability thresholds (Lewis, Szava-Kovats and Pärtel, 2016).

In paper **II**, to include the maximum amount of co-occurrence information, I used the whole dataset to estimate the indication matrix between pairs of taxa. To obtain conservative discrete dark diversity estimations, I only kept taxa with greater than 90% probability according to the hypergeometric method. In addition, for any given time, I only considered as part of dark diversity of sedimentary pollen those taxa recorded in any sample during a 500-year time window. Such a filter defined dark diversity without considering taxa that have either not yet arrived to the region or have gone regionally extinct. To assess how realized the local biodiversity was in each local site, excluding the effects of environmental filtering, I also calculated taxonomic completeness for each sample as follows: log(observed diversity/dark diversity).

## 2.3 Functional traits

Different functional traits linked to species dispersal, establishment and persistence were considered in this thesis. In paper **II**, I considered clonality, maximum height, specific leaf area (SLA) and seed weight, retrieved from Reitalu *et al.* (2015; 2019) whereas in paper **III**, I considered the three most used functional traits of lichens related to growth form, photobiont type and reproductive strategy, retrieved from ITALIC 5.0 (Nimis and Martellos, 2017).

Clonality is linked to species persistence and favours short-distance dispersal of plants (Klimešová *et al.*, 2021). Plant height and seed weight are linked to species dispersal, establishment and persistence (Westoby, 1998). Taller plants have usually higher competitive and dispersal abilities, whereas large-seeded species typically produce fewer seeds but have stronger establishment ability and disperse over longer distances, when having efficient vectors (i.e. animals, water etc.) (Howe and Smallwood, 1982; Nathan *et al.*, 2008; Muller-Landau, 2010). SLA is mostly related to stress tolerance, with species having low SLA being more conservative in resource use (high-stress tolerance), whereas species with high SLA are usually fast growing but have lower stress tolerance (Reich, 2014). For lichens, growth form and photobiont type are related to changes in forest light and humidity, while reproductive strategies are directly connected with lichen dispersal ability and establishment (Nascimbene and Spitale, 2017). Each lichen species can belong to a single category (trait value) in each of these traits. For example, regarding growth form, lichen species have either crustose, foliose or fruticose form. I calculated the proportion of each trait value in each site both for observed and dark diversities.

## 2.4 Introducing the Functional Dark Diversity

In paper **II**, to characterize the multidimensional functional trait space of observed and dark diversity, I first log-transformed the trait data and performed a principal component analysis (PCA) with the scaled trait values for each taxon. I used both first and second PCA axis (which explained 71% of the total trait variation) to define a two-dimensional functional space. Further, I used the scores of taxa in these components as indicators of the functional traits of taxa. I then estimated a trait probability density function (TPD) for each taxon as a bivariate normal distribution centred in the scores of the taxon and with a standard deviation (bandwidth) that was chosen using the plug-in bandwidth selector available in the 'ks' R package (Duong *et al.*, 2022). Using the TPDc function from R package 'TPD' (Carmona *et al.*, 2019), I combined (i) the TPD functions of the taxa present in each sample and (ii) the TPD functions of the taxa classified as belonging to dark diversity samples, obtaining TPD functions for the observed and dark diversity of each sample, respectively, and applied a 99% probability threshold to these TPD functions, estimating the amount of functional space occupied by observed and dark diversity in each community at each time period (functional richness). Since the functional dark diversity corresponds to the suitable functional space not locally occupied, I overlapped the functional space occupied by both observed and dark taxa and considered only the unique portion of this overlapped functional space as the functional dark diversity (Figure 2 – bottom panel). Similarly to taxonomic completeness, I calculated functional completeness as log(functional observed diversity/functional dark diversity).

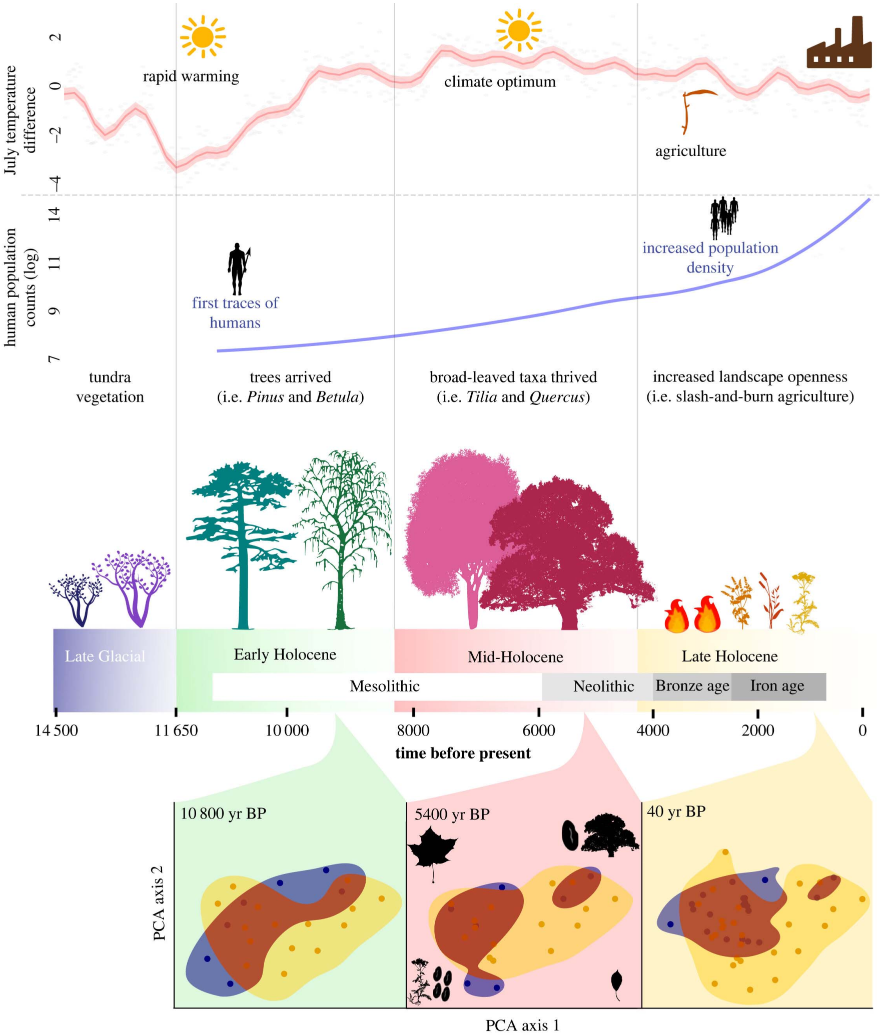

**Figure 2**. Conceptual figure depicting how climate, human impact, vegetation dynamics and the functional space of plants changed over the past 14 500 years in northern Europe. Different time periods are depicted with different colours: Late Glacial (in blue); Early Holocene (in green); Mid-Holocene (in red); Late Holocene (in yellow). Over time, different climatic (warming period and climatic optimum) and starting point of major human impacts (first traces of humans, beginning of agriculture, increasing population density and modern period), as well as vegetation dynamics are depicted and were reported in different palaeocological studies in northeastern Europe. Bottom panel represents the functional space occupied by taxa in observed and dark diversity (yellow and blue area and points, respectively) in a single site over three different periods (Early Holocene, Mid-Holocene and Late Holocene). The functional space is represented by a PCA (two axis), in which the first axis was composed by taxa (points on the graphs) ranging from high stature and seed weight to the opposite traits values and the second axis ranging from small to large leaves. Since dark diversity is defined as the set of species suitable but locally absent, I calculated the functional dark diversity as the area of suitable but locally absent trait space (only the area not overlapping with observed trait space – blue area). Temperature trend (GAM fit line in red and 95% confidence interval – shaded area) was calculated as the difference of July temperature of each year from pre-industrial July temperature mean. Human population trend (in blue) depicts human population estimates (inhabitants/grid cell (10 km) – log-transformed). Modified from Figure 1 in **II**.

## 2.5 Statistical analysis

In paper **II**, I used generalized additive models (GAMs) to identify how taxonomic and functional observed diversity and dark diversity, species pool size, and community completeness, as well as mean trait values changed over time. Accordingly, six GAM models were built, using Age (calibrated years before present, fitted using a cubic spline smoother) as the independent variable in all models. In the models in which the independent variable could be estimated for each diversity component (observed diversity, dark diversity, species pool), I used the diversity component as a factor, so that a separate smoother was created for each diversity component, allowing to describe differences in the temporal patterns of the different components. GAM models were done using the R package 'mgcv' (Wood, 2022).

In paper **III**, I used linear regressions to test how observed and dark diversity, species pool size, and community completeness changed along the elevational gradient. Observed diversity, dark diversity and species pool size were log-transformed. Since elevation and temperature are highly correlated (0.94 – Appendix S4 in **III**), I chose elevation as the predictor variable. To examine differences in trait value proportions between observed and dark diversity and to test whether these proportions change along the elevational gradient, I used linear Dirichlet regressions (Douma and Weedon, 2019), since this technique is suitable to test proportion differences between groups. Dirichlet regressions models included diversity type (observed or dark diversity), elevation, and their interaction as predictors. Analyses were done with the DirichReg function of the R package 'DirichletReg' (Maier, 2014), and the direction of patterns observed along the elevational gradient were plotted using predicted values with 95% confidence intervals generated from bootstrapping with 1000 randomizations (Douma and Weedon, 2019).

# 3 RESULTS

## 3.1 Global change effects on observed and dark diversity

In paper **I**, I reviewed how global change effects may impact species in observed and dark diversity, and proposed that observed and dark diversity enabled to decompose species gains and losses in four different biodiversity flows: local gain (species moving from dark to observed diversity); local loss (species moving from observed to dark diversity); species pool gain (suitable species immigrating to the region, or being incorporated to dark diversity due to change in ecological conditions in the study site) and species pool loss (species in dark diversity or in extinction debt at observed diversity going extinct from the region, or becoming unsuitable for the site due to change in ecological conditions) (Figure 3). Theoretically, more local and species pool gains are expected in observed and dark diversity towards benign conditions.

In paper **II**, both taxonomic and functional observed and dark diversity of plants increased in towards benign conditions in northern Europe: warmer climates after the Late Glacial Period and more habitat heterogeneity during the Late Holocene.

In paper **III**, observed diversity ($R^2 = 0.75$), dark diversity ($R^2 = 0.19$), species pool size ($R^2 = 0.80$) and community completeness ($R^2 = 0.15$) of lichens, increased towards more suitable conditions for lichens (i.e. cooler sites) along an elevational gradient in northern Italy (Figure 4 – see statistics in Appendix S1 in **III**).

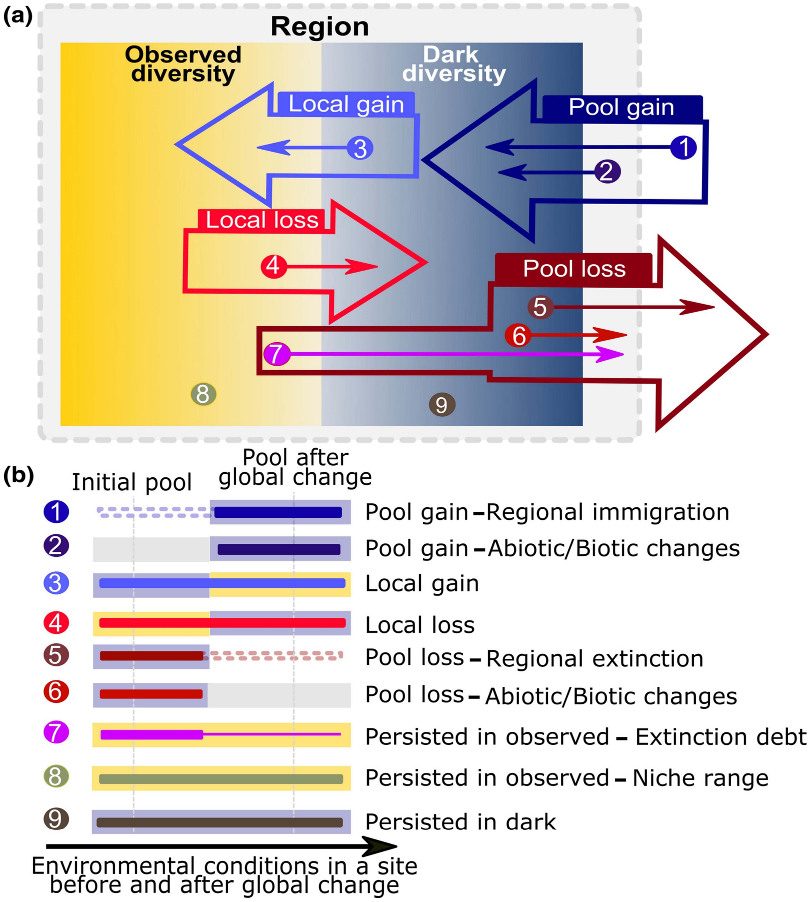

**Figure 3**. Gains and losses of observed and dark diversity (currently absent suitable species) of a local site. Species are indicated by coloured circles and numbers. (a) Observed diversity can increase only if it gains species from dark diversity (local gain) and decrease when species 'move' to dark diversity (local loss). Changes in environmental conditions can make some observed diversity species unsuitable and these will be gradually excluded both from observed diversity and species pool when their extinction debt is paid (species 7). Dark diversity is additionally gaining and loosing species when site-specific species pool changes (pool gain and loss). (b) Species gain and loss in observed and dark diversity of a single site before and after global change. x-axis represents an ecological gradient, with the vertical lines showing the conditions of a site before and after global change. y-axis represents species (each characterized by a colour and a number) with different ecological requirements (niche), indicated by the horizontal bars. At each given time, species whose requirements overlap with the current local conditions and are present in the region can be either locally present (observed diversity) or absent despite being suitable (dark diversity). After global change, some species can also be locally present despite not being suitable anymore (extinction debt, thin line at species 7). Furthermore, some suitable species can be absent from the region at the considered time due to regional immigration or regional extinction (dashed lines at species 1 and 5). Background colours depict species present in observed diversity (orange), dark diversity (blue) and in the region (grey). Copy of Figure 1 in **I**.

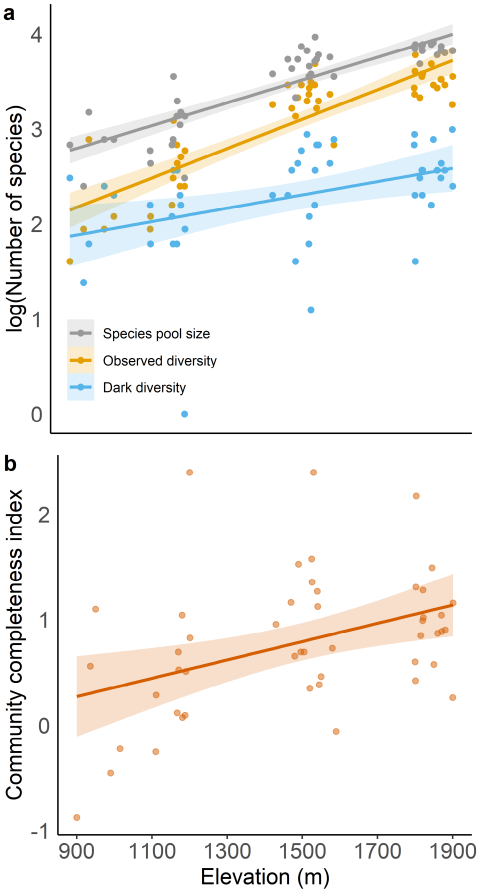

**Figure 4**. Observed diversity, dark diversity and species pool size (a) and community completeness index (b) of epiphytic lichens along an elevation gradient in spruce forests of northern Italy. Regression lines fitted by applying a linear regression. Shaded areas depict 95% confidence intervals. Modified from Figure 1 in **III**.

## 3.2 Observed and dark diversity dynamics under global change

The different biodiversity flows presented in paper **I** are expected to face different temporal lags (Figure 3). Theoretically, local losses are expected to be slower, since all individuals from a particular species need to disappear from the local site. Species pool gains and losses are expected to be faster since the suitability of species in dark diversity is mostly dependent on the environmental conditions, dispersal capacity and biotic interactions. Local gains can be either fast, when species arrive and become part of the local site, or slower, when species persist in dark diversity (expansion lag) (Figure 3).

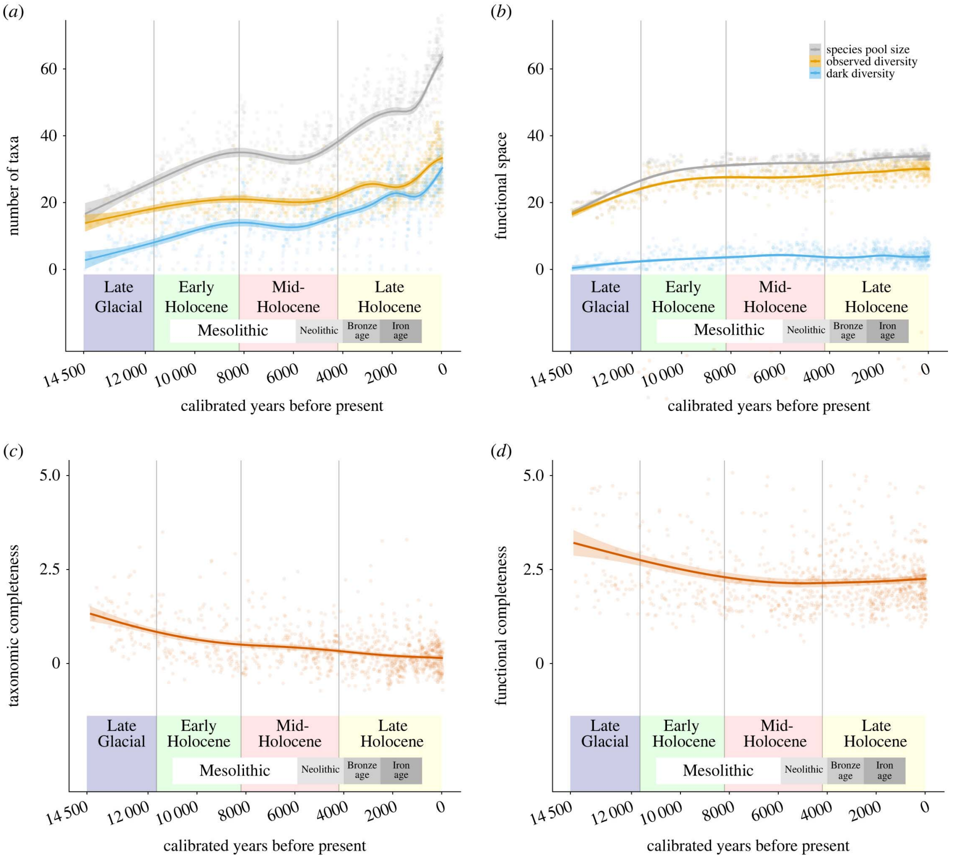

**Figure 5**. (a) Number of taxa, (b) functional space in both observed and dark diversity, as well as (c) taxonomic and (d) functional completeness of sites in northeastern Europe over the past 14 500 years (cal. yr BP). Lines represent the fits of GAM and shaded areas the 95% confidence intervals. Copy of Figure 2 in **II**.

In paper **II**, taxonomic observed and dark diversity increased over millennial time scales in Northern Europe (local and species pool gains) ($R^2 = 0.81$, $p \leq 0.001$; Table S2 in **II** for full statistical results), but dark diversity increased generally faster, with a sharp increase from 500 cal. yr BP (Figure 5a), being confirmed by the decreasing community completeness trend ($R^2 = 0.19$, $p \leq 0.001$; Table S3 in **II** for full statistical results).

Taxonomic completeness decreased from the Late Glacial towards the Early Holocene, became stable during the transition between the Early Holocene and Mid-Holocene (approx. 8,300–7,000 yr BP) and continued decreasing from the Mid-Holocene until the present (Figure 5c).

Functional observed and dark diversity increased over time ($R^2 = 0.97$, $p \leq 0.001$; Table S4 in **II** for full statistical results). Specifically, functional observed diversity increased after the Late Glacial, did not change from 10,000 cal. yr BP until 5,500 BP, and increased again during the Late Holocene. Functional dark diversity increased after the Late Glacial until the end of the Early Holocene, became stable during the Mid-Holocene, slightly increased again during the Late Holocene (approx. 2,000 cal. yr BP) and decreased afterwards (Figure 5b).

Functional completeness decreased from the Late Glacial towards the Early Holocene and stayed roughly stable over the Mid-Holocene and Late Holocene (Figure 5d; $R^2 = 0.05$, $p \leq 0.001$; Table S5 in **II** for full statistical results).

## 3.3 Functional traits explain why species are in dark diversity

In paper II, compared to taxa in observed diversity, taxa in dark diversity had generally lower scores in the first PCA axis (related to short stature, lighter seeds and higher clonality ability; $R^2 = 0.70$, $p < 0.01$), and higher scores in the second axis (related to large SLA; $R^2 = 0.50$, $p < 0.01$). After the Late Glacial period, taxa became taller, with larger seeds, lower clonality ability and larger leaves.

In paper **III**, compared to observed diversity, species in dark diversity had higher proportions of crustose and fruticose forms, presence of green algae, and sexual reproductive strategy. Along the elevational gradient, there was an overall increase in foliose and fruticose forms, proportion of the green algae type and an overall increase in the proportion of asexual reproductive strategy in expense of the sexual one. When the interaction was considered, crustose form proportion decreased more in dark than in observed diversity along the elevation transects. The fruticose form proportion was lower in dark than in observed diversity at lower elevations, but higher at higher elevations (Figure 6a) Variation in the proportions of photobiont types in observed and dark diversity did not differ along the elevational gradient (Figure 6b). There was no difference in the variation in the proportions of reproductive strategies in observed and dark diversity along the elevational gradient (Figure 6c).

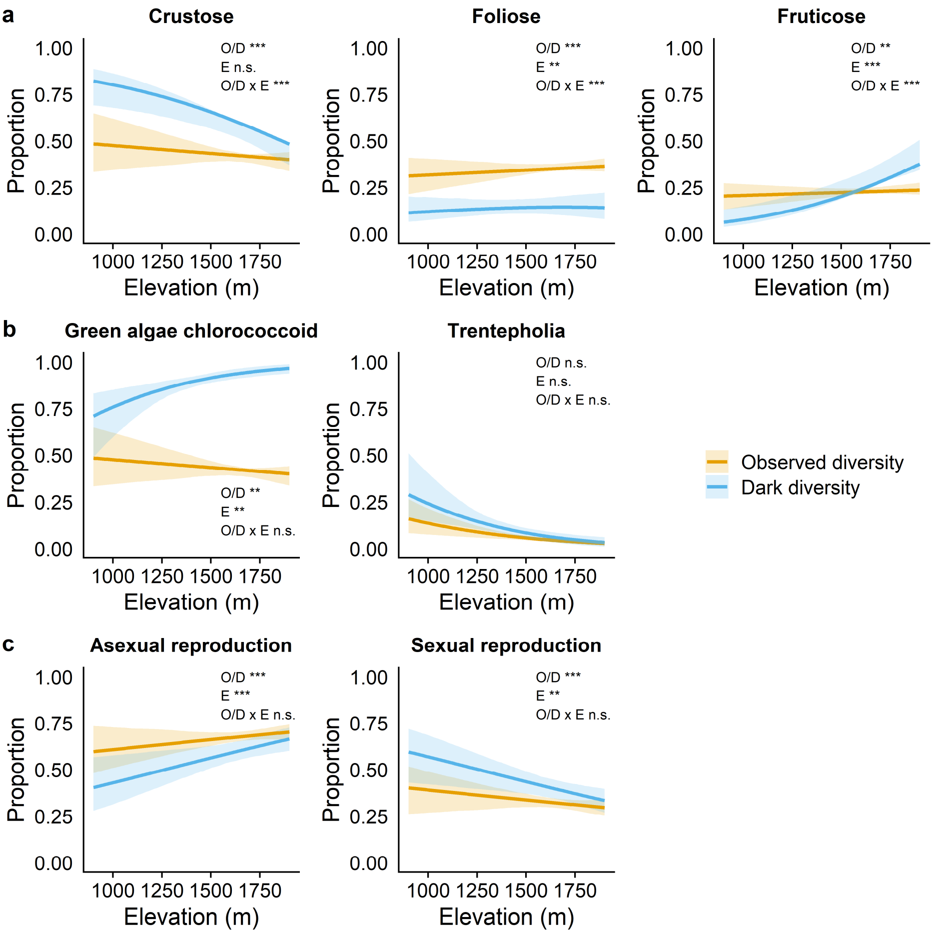

**Figure 6**. Change in proportion of functional traits of epiphytic lichens in observed and dark diversity along an elevational gradient in spruce forests of Northern Italy. Solid lines depict mean predicted values from the bootstrapping (1000 randomizations). Dirichlet regression models, whereas shaded areas depict the confidence intervals (lower = 0.025, upper = 0.975). Annotations in panels inform whether the models are significant (*p < 0.05, **p < 0.01, ***p < 0.001) or non-significant (n.s. p≥0.05) among observed and dark diversity (O/D); along the elevation (E); and their interaction (O/D × E). Modified from Figure 2 in **III**.

# 4 DISCUSSION

Dark diversity is an important concept to understand how ecological communities are assembled across scales, by depicting how the filtering process works from regional to local scales. However, given that global change drivers affect community assembly processes across space and time, prior to this thesis no studies had explored, theoretically and empirically, whether dark diversity can be useful to examine biodiversity change dynamics, creating a link between spatial and temporal scales. Those dynamics are relevant because they may improve the way we quantify and assess biodiversity change, and, consequently, enhance nature conservation. In this thesis, I advanced the role of dark diversity as a complementary and promising tool to examine biodiversity change by developing a conceptual framework in which species gains and losses are decomposed within the species pool (**I**); testing how much and how fast both taxonomic and functional species pool dynamics changed over time, due to climate change and human impact (**II**); and how dark diversity can be used to enhance nature conservation of species threatened by extinction, using lichens as a model (**III**).

## 4.1 Global change effects on observed and dark diversity

Climate and land-use changes affect the way species disperse, cope with new environmental conditions and biotic interactions, affecting both species and traits present in the local community, but also its dark diversity. In theory, I suggested that these changes can lead to species gains and losses at the local site but also at the species pool level, potentially changing the whole species pool configuration (**I**). When those changes turn the environment towards more benign conditions, increases in both observed and dark diversity are expected. Here I confirmed those assumptions by showing that whenever the environmental conditions become less harsh, due to climate warming after the Late Glacial period and more habitat heterogeneity during the Late Holocene (**II**), or due to increasing cooling and moisture along an elevational gradient (**III**), both observed and dark diversity of plants (**II**) and lichens (**III**) increased. Those increases likely occur because harsh environments act as strong environmental filters, in which only a small portion of the regional diversity is suitable. Benign conditions, however, enable the creation of different niches, allowing more species to establish locally, and, consequently, both observed and dark diversity (Karger *et al.*, 2015; Paquette and Hargreaves, 2021).

Although the species pool sizes of both plant and lichen communities increased towards benign conditions, community completeness showed a divergent pattern, decreasing for plants and increasing for lichens. The implications of such a mismatch need to be addressed with some caution since they were examined in different contexts. However, different studies have suggested that species pool size and community completeness are likely to be driven by different processes, with species pool size being more affected by regional processes (i.e. environmental filtering), and community completeness by local ones (dispersal and biotic interactions) (Ronk, Szava-Kovats and Pärtel, 2015; Riibak *et al.*, 2017). For example, species pool sizes of AM fungi are more strongly related to historical biome distribution, whereas community completeness are more related to the degree of wilderness in each local site (Pärtel *et al.*, 2017). Likewise, both observed and dark diversity of plants increase towards warmer sites along the latitudinal gradient in Europe, but community completeness is more affected by local anthropogenic disturbances, being higher in less disturbed areas (i.e. mountainous regions) (Ronk, Szava-Kovats and Pärtel, 2015). Thus, the mismatch between completeness patterns towards benign conditions in both plants and lichens could be partially explained both by regional and long-term factors driving the species pool size, and more local ones (e.g. dispersal and human impact) driving the community completeness. In other words, although benign conditions increased the suitability of both lichen species and plant taxa (larger species pool), anthropogenic disturbance for lichens was also lower at more benign areas, enabling more species to establish locally. For plants, human impact increased during the Late Holocene, favouring some taxa but potentially hampering the establishment of several other taxa (decreasing the community completeness).

Future global change scenarios are expected to make environmental conditions harsher (e.g. climate extremes, increasing aridity etc.), which will potentially cause the shrinking of species pool sizes, due to both local and species pool losses (Jacobsen *et al.*, 2012; Atkinson *et al.*, 2021). Given that dark diversity usually mimics observed diversity patterns towards benign conditions, but community completeness do not, mapping how both observed, dark diversity and completeness are changing in the Anthropocene is important to detect threatened species that are likely to go regionally extinct, as well as newcomers becoming suitable (both native and non-native). For instance, recent studies have shown that dark diversity helps identifying warming sensitive species mostly threatened to go extinct (Dalle Fratte *et al.*, 2022), as well as highly invasive species appearing in local sites in both Europe and North America (Paganeli *et al.*, 2022). Community completeness can then be used to test how resistant those local sites are, since more complete sites are expected to be more resistant against invasion (Bennett *et al.*, 2016).

## 4.2 Global change and species pool dynamics

Over time, dark diversity depicts species delaying in colonizing or establishing in a suitable local site, revealing which species are experiencing expansion lags in their expansion range and, thus, how fast species pools are changing (**I**, **II**). As predicted in theory (**I**), constant increases in dark diversity should also lead to increases in observed diversity. This pattern is shown for both taxonomic and functional observed and dark diversity of plants in Northern Europe over the last 14,500 years (**II**). Accordingly, I show that, over time, taxonomic dark diversity increased generally faster than observed, indicating that several taxa appearing over time persisted in dark diversity of most potential sites for centuries, not expanding their geographical range.

Different studies have shown that biodiversity has tracked climate changes relatively fast in the past. However, several species presented expansion lags, mostly due to dispersal limitation, and some of those lags still persist until nowadays (Svenning and Skov, 2007; Svenning, Normand and Skov, 2008; Rijal *et al.*, 2021). Here I show that dark diversity can be used as a tool to track those lags in establishment and dispersal of species. For instance, the faster increase in taxonomic dark diversity compared to observed diversity suggests that climate and human activities increased the number of sites suitable for many taxa faster than what potential biodiversity could realize locally, indicating expansion lag. By assessing the frequency of taxa in observed and dark diversity it is possible to identify that many locations became suitable to some taxa, but these taxa persisted in expansion lag (i.e. *Brassicaceae*, *Frangula*, *Plantago lanceolata*; Figure S5 in **II**). After the introduction of agriculture and, consequently, more heterogeneous landscapes, several of those species moved from dark diversity to observed diversity (local gains), expanding their geographic range centuries later.

In this thesis I presented functional dark diversity as the set of traits suitable in the region but not locally realized. Although taxonomic dark diversity increased faster than observed diversity, the same was not true for the functional facet. Instead, over the Holocene most of the functional expansion came from the taxa becoming part of the observed diversity. First, this result indicates that as soon as niches were created, after the Late Glacial period and during the Late Holocene, some taxa colonized and established locally, with relatively no functional expansion lags (Fukami, 2015). Second, this result also indicates that the rapid increase in taxonomic dark diversity was mostly due to functionally redundant taxa that had to compete with functionally similar ones already occupying their niche. Such a functional redundancy at the species pool level can be an indication of high stability or resilience of ecosystems, since taxa displaying similar functional roles, although locally absent, were suitable and present in the surrounding, being potentially able to buffer local losses (Biggs *et al.*, 2020; Auber *et al.*, 2022).

After the onset of important environmental changes, decreases in observed diversity were also predicted in theory due to extinction debt (**I**). However, this pattern could not be detected using the examined dataset. This could be partially explained by the increasingly benign conditions over time, increasing both observed and dark diversity, which may have hindered the predicted effects of extinction debt. In addition, it is likely that the extinction debt was more evident at single local sites or specific taxa (Hylander and Ehrlén, 2013). For example, looking at the frequencies of some taxa in both observed and dark diversity, it is possible to identify some taxa decreasing their frequencies both in observed and dark diversity after the onset of an extreme environmental change (i.e. rapid warming after the LG), which could be an indication of extinction debt (i.e. *Dryas*, *Thalictrum*, *Urtica* – figure S5 in **II**). However, this pattern requires further investigation to test whether those decreases were, in fact, related to extinction debt effects or not.

## 4.3 Linking dark diversity to functional traits

Functional traits were key to understand why species were in dark diversity and presented expansion lags. Accordingly, over time, when compared to observed diversity, environmental and biotic filters mostly hampered plant taxa that were functionally redundant and displaying fast life-history strategies: lower height, lower seed weight and higher SLA, which might be linked to dispersal limitation and stress intolerance (**II**). For lichens, however, the traits mostly found in dark diversity were those related to warming sensitivity and dependency of a mutualist, highlighting that dispersal may not be always the most important driver keeping species suitable but absent, especially for organisms that rely on strict biotic interactions (**III**).

Dispersal limitation and stress tolerance are often reported as the most important drivers keeping plant species in dark diversity (Riibak *et al.*, 2017; Moeslund *et al.*, 2017). Here I show that those drivers were also important over millennial time scales and helped explaining why taxa delayed in colonizing and establishing locally, not expanding their geographic range. For instance, prior to the intensification of agriculture, ruderal and grassland taxa arrived in the region, occupied some sites, and persisted suitable but absent in many other sites (e.g. *Asteraceae*, *Melampyrum*, *Rumex*, *Saxifraga*). A similar pattern was reported in North America, in which taller and large-seeded species were more likely to have tracked climatic changes over the Holocene, potentially due to the dispersal by large mammals and birds (Knight *et al.*, 2019; Butterfield *et al.*, 2019). Such a pattern reinforces the notion that, when global changes make environmental conditions less harsh and both observed and dark diversity increase, plant species with high dispersal abilities and higher stress tolerance tend both to arrive first and persist longer in those habitats (Fukami 2015).

Over the last 2,000 years, however, with the intensification of agricultural practices, some taxa facing expansion lags were able to move from dark diversity to observed diversity of several potential sites (e.g. herbaceous and ruderal taxa) (Reitalu *et al.*, 2015). Thus, although taller and large seeded taxa thrived after the Late Glacial period, potentially due to their high dispersal and persistence abilities, by comparing the functional traits in observed and dark diversity over the last 2,000 years, it was possible to identify that such a pattern is changing. This indicates that human impact has been playing an important role in changing the functional profile of the species pool in northern Europe over the last few millennial. This pattern is still captured in contemporary examination at the European scale, suggesting that human impact is mostly favouring the local establishment of species with small seeds nowadays (Riibak *et al.*, 2017).

Traits related to stress intolerance were also key to explain the dark diversity of lichens, but species with higher dispersal ability were also more often in dark diversity, creating a mismatch in the trait patterns between plants and lichens. Since lichens are sensitive to warming, traits related to warming sensitivity are expected to be found more often in dark diversity. However, the dispersal ability mismatch can be explained by their high mutualistic dependency. For example, although asexual lichens usually display low dispersal abilities, they do not depend on a partner to be able to establish (Belinchón, Yahr and Ellis, 2015). However, species displaying sexual reproduction require a photobiont partner already locally established, yielding a strong biotic filter and explaining why they are more often in dark diversity. Although such a mismatch was unexpected, studies examining mycorrhizal association and dark diversity of plants have shown that plants displaying obligatory association with mycorrhiza are also more often found in dark diversity (Moeslund *et al.*, 2017; Paganeli *et al.*, 2022). Likewise, plants species with high dispersal abilities can be more often found in the dark diversity of sites in fragmented landscapes due to higher chances of arriving in unsuitable locations (Riibak *et al.*, 2020). It is likely that the same reasoning applies to explain the dark diversity of lichens with high dispersal ability that need a photobiont partner already available locally.

## 4.4 Dark diversity, global change and nature conservation

In paper **I**, I suggest that dark diversity offers a window of opportunity to both protect and restore species, by separating species still locally suitable from those that are not part of the local species pool anymore. In paper **III**, I tested this idea using lichens and elevational gradients as models, and integrating dark diversity, functional traits and community completeness. I show that epiphytic lichens are under threat due to climate change in both edges of the elevational gradient, but their extinction risk depends on a certain combination of traits. For instance, at low elevations, harsh conditions yield a small species pool size, with relatively more species in dark diversity (low completeness), requiring short-term restoration actions in order to facilitate the establishment of some species in dark diversity. This restoration can be focused on crustose species since they are in high proportion in dark diversity and considered more warming resistant. However, since global warming will affect low elevations more rapidly and current conditions are already harsher, long-term conservation strategies should focus on the entire species pool to prevent species losses in both observed and dark diversity (**III**).

Climate change will affect both local diversity and composition of lichen species (Escolar *et al.*, 2012; Hauck, Bruyn and Leuschner, 2013) and, by being warming-sensitive, the local extinction of lichens is considered relatively fast, whereas their recolonization might take several years (Johansson, 2008). Thus, at high elevations, conservation and ecosystem management is needed to prevent local losses, given the high community completeness in those areas (relatively less species potentially able to buffer local losses), focusing on macrolichens and species displaying sexual reproduction, due to their warming sensitivity and establishment limitation. Likewise, conservation priority should focus on larger mountain forests, due to their higher species pool size (Martellos *et al.*, 2020), and on maintaining microclimatic conditions (e.g. non-intensive forest management), attenuating future macroclimatic changes and potentially decreasing species loss (Nascimbene, Nimis and Dainese, 2014).

Although not the focus of paper **II**, dark diversity patterns can also shed some light on the importance of monitoring species pool dynamics to enhance nature conservation. For example, in paper **II**, the decrease of conservative taxa in observed diversity over the last 2,000 years indicates that human impacts are mostly favoring resource-acquisitive ones, which is a pattern also validated in contemporary datasets (Riibak *et al.*, 2017). These changes in the trait profile have important evolutionary and ecological implications that deserves further examination, especially for nature conservation, since they potentially affect important ecosystem services and processes, including accelerating nutrient cycling, increasing productivity and biomass turnover, as well as herbivory and sensitivity to drought events (Diaz and Cabido, 1997; Erb *et al.*, 2016; White *et al.*, 2022). Importantly, although all these processes can be examined using the observed diversity only, here I show that by using dark diversity it is possible to examine how the whole species pool is changing, enabling a broader conservation management. Moreover, the lack of functional expansion lag in **II** suggests that examining the functional space of the species pool can be an important tool for tracking harmful species with highly invasive trait characteristics (Paganeli *et al.*, 2022). For instance, invasive species becoming part of the dark diversity of local sites, occupying unique portions of the functional space and displaying good dispersal ability, should be priority of conservation management to delineate strategies to ensure these species persist absent (Lewis *et al.*, 2017).

Future global changes impose important challenges to both conservation and restoration practices. For instance, current protected areas are mostly settled based on current species niches and distribution areas (Hanson *et al.*, 2020; Ludovicy *et al.*, 2022). However, global changes will modify those niches, potentially forcing the movement of several species out of protected areas (Hanson *et al.*, 2020). In addition, current restoration activities usually face difficulties in knowing what species and traits are more suitable to the current local conditions (Harris *et al.*, 2006; Lewandrowski *et al.*, 2021). Examining species and traits in dark diversity can potentially assist in both designating conservation areas as well as guiding restoration activities in a global change scenario, since it provides an initial list of potential species and traits suitable locally (Lewis *et al.*, 2017; Noreika, Pärtel and Öckinger, 2020). However, empirical examination is still required, which will be potentially achieved with local experiments. For example, classical experiments have tested the role of dispersal limitation in structuring local communities by adding seeds to those sites (Münzbergová and Herben, 2005; Myers and Harms, 2011). Following a similar idea, recent initiatives have started adding seeds of species in dark diversity to local sites, testing whether there is a correlation between high dark diversity probability and establishment success (Pärtel *et al.*, 2019 – SEED-DarkDivNet).

# 5 CONCLUSIONS

In this thesis I show, both theoretically and empirically, that taxonomic and functional dark diversity are important tools to assess biodiversity change and enhance nature conservation across space and over time.

1: Observed and dark diversity of both plants and lichens generally increased towards more benign conditions, reinforcing that less harsh environmental filters increase the number of available niches, leading to local and species pool gains. Specifically, in the case of plants, climate warming after the Late Glacial period and human activities during the late Holocene were key drivers of local and species pool gains. For lichens, decreasing warming conditions along the elevational gradients increased gains in both observed and dark diversity. These results suggest that the expected future climatic conditions will impose harsher environmental conditions, leading to higher local and species pool losses for both plants and lichens, shrinking the species pool size of both taxonomic groups (**I, II, III**).

2: Dark diversity can improve our understanding of biodiversity dynamics under global change by revealing species becoming both locally extinct and locally suitable but absent. This information enables to track changes in the species pool, creating windows of opportunities both to protect or restore biodiversity across scales and over time. Dark diversity successfully depicted taxa in expansion lags over the Holocene, indicating that species becoming suitable after the Late Glacial period and during the Late Holocene were mostly persisting in dark diversity, not realizing locally. This faster increase in dark diversity for the taxonomic facet was not mirrored by the functional facet. Instead, during the Late Holocene the expansion of the functional pool came mostly from taxa in observed diversity. These results indicate that (i) as soon as niches were created taxa with higher dispersal capacity and stress tolerance were able to rapidly fill the vacant niche, revealing relatively no functional expansion lags; and (ii) most taxa becoming part of dark diversity were functionally redundant. The high functional redundancy at the species pool level, can be an indication of high stability and resilience of local communities, since taxa in dark diversity were in the region, locally suitable, and playing similar functional roles as species observed locally, being able to buffer local losses (**I, II**).

3: Functional traits revealed why species were in the dark diversity of both plants and lichens, and in expansion lag. On one hand, fast life history traits, linked to low dispersal ability and stress intolerance, explained the dark diversity of plants over millennial scales in NE Europe and why those taxa became suitable but did not realize locally. On the other hand, functional traits related to climate sensitivity and low establishment ability were key to explain the dark diversity of lichens along an elevation gradient in NE Italy. The mismatch between plants and lichens related to dispersal and mutualistic traits highlight that different drivers act in driving the dark diversity of different organisms, suggesting that organisms relying on strict biotic interactions can face additional filters in that matter (**II, III)**.

4: Dark diversity and functional traits can be used to guide nature conservation plants, providing a broader conservation planning by focusing on the whole species pool (observed and dark diversity together). Using lichens as a model organism and elevational gradients as a proxy of climate change, I show that lichens are threatened at both ends of the elevational gradient due to climate warming predictions. At low elevations, due to low species pool size and completeness, both short-term restoration activities and long-term conservation efforts focusing on the whole species pool are needed. Towards higher elevations, conservation should be the priority, given that expected warmer conditions will impose important threats to macrolichens (foliose and fruticose), and species with sexual reproduction strategy, either due to their lower proportion in dark diversity, higher sensitiveness to climate change and establishment limitation. In this thesis, I suggest that integrating dark diversity and functional traits is a novel and cost-effective method to protect and restore biodiversity, since it provides an initial list of species and traits that should be focused on, as well as create windows of opportunities to restore needed and suitable functions, preventing regional extinctions (**I, III**).

# SUMMARY

Global changes (e.g. climate trends and land use transformations) modify the way species disperse between and within regions, assemble to ecological communities, and interact locally. However, species often react to changes with a time delay, and information on observed species and functional traits in a local site might provide limited information about ecosystem integrity. Here I suggest that this information gap can be filled by considering the local site's dark diversity – the set of species and traits locally suitable, potentially able to reach the site but still being absent. Observed and dark diversity together constitute the site-specific species pool, describing the portion of the regional taxonomic and functional diversity which is relevant to a given study site.

Assessing how global change drivers are affecting both observed and dark diversity might be key to quantify and forecast biodiversity change across spatial and temporal scales. Although the dark diversity concept had been repeatedly used to depict how local communities are assembled, no studies had directly examined the effects of global changes on the species pool dynamics prior to this thesis. Here I demonstrate how dark diversity can be useful to simultaneously assess biodiversity changes across large-scale environmental gradients and millennial time scales.

Taxonomic dark diversity depicts how many species are suitable but absent in a particular site. Adding information on functional traits helps to understand why species are suitable but absent, revealing how different filters operate from regional to local scales. Moreover, variation in single functional traits can be analysed in combination and summarized by calculating the functional observed and dark diversity of local communities. Functional dark diversity is then the portion of the functional space that could be theoretically locally occupied but is absent; this information can help to understand how functionally redundant the whole species pool is.

By revealing the set of suitable but locally absent species and traits in the surrounding region, dark diversity links regional and local scales, and enables calculating how complete each local site is (community completeness index). By examining the composition of observed and dark diversities over time, we can identify local dynamics (species "moving" between observed to dark diversity), as well as new species in the region becoming suitable or disappearing from the whole region. The community completeness can be assessed over time to examine how the species pool is changing. For example, if both observed and dark diversity increase over time but dark diversity is increasing more and faster, the community completeness will decrease, meaning that more species are becoming suitable but they are not realizing locally. Assessing how much, how fast and in what direction species pools are changing can provide important information on how climate and land use changes affect biodiversity across scales. Functional traits can potentially explain why those species are delaying in establishing locally, and this knowledge is vital for nature conservation. For instance, with

dark diversity one can track species and traits threatened by regional extinction, providing a list of species that should be conserved, or species and traits that are suitable and could be locally restored.

Dark diversity can be examined at the site level using the community completeness, informing which sites should be restored (low completeness) or conserved (high completeness). This is because low complete sites have many potential species in dark diversity that could realize locally, and high complete sites have fewer potential candidates to buffer local losses. In this thesis I used both theoretical and empirical approaches to test how global changes may affect both taxonomic and functional observed and dark diversity, and how to use this information to enhance nature conservation of warming sensitive species, using lichens and elevational gradients as model. Dark diversity offers opportunities to advance the way we examine community assembly and biodiversity change in the Anthropocene. For example, it enables decomposing species gains and losses within the species pool framework. At the local site, such a framework reveals species moving from dark diversity to observed (local gains), and species becoming locally extinct but still suitable (local loss). At the species pool level, one can detect species that became unsuitable (species pool loss), and those that became suitable but could not yet colonize or establish locally (species pool gain). This information can then be used, for example, to examine how fast species pools are changing.

By examining the dark diversity of sedimentary pollen over time, I show that over the Holocene global changes created more benign conditions, boosting the number of taxa in Northern Europe, increasing both observed and dark diversity gains. However, most of the taxa becoming suitable were persisting in dark diversity, not realizing locally, indicating an extensive expansion lag in taxa's geographic range. For instance, after the Late Glacial period (warmer conditions) and Late Holocene (human impact, increased niche availability) several taxa appeared in dark diversity and took centuries to realize locally. I integrated functional traits to understand both why those taxa were in dark diversity as well as presented expansion lags over time. By comparing the functional diversity and mean trait values in observed and dark diversity, I found that such an expansion lag was mostly related to the high functional redundancy of taxa in dark diversity, as well as their dispersal limitation and stress intolerance. Thus, although several taxa were becoming suitable to local site's conditions, most of those taxa in dark diversity had to compete with good disperses and stress tolerant taxa already occupying their potential niche.

Functional traits in observed and dark diversity were key to inform what groups we should focus on, enhancing nature conservation efforts, and how different species may respond to global changes. For instance, along elevational gradients, I show that the dark diversity of lichens was mostly composed by species displaying traits related to climate warming sensitivity and mutualistic association. Likewise, lichens were threatened at both extremes of the gradient. At lower elevations (warmer locations), the species pool size and completeness were low, indicating that both short-term restoration and long-term conservation efforts are needed to attenuate future climate warming effects. Accordingly, I suggest that lichens with crustose characteristics should be the focus of restoration activities since they are in higher proportions in dark diversity at lower elevations. In cooler locations, conservation efforts are more needed to decrease the chances of local and regional extinction of macrolichens and species with sexual reproduction, since they are both warming sensitive and presented establishment limitations.

Understanding how fast climate change and human impact have affected biodiversity in the past and might continue to affect biodiversity in the Anthropocene is a longstanding issue in ecology. In this thesis I describe the use of dark diversity concept as a complementary and novel approach to examine biodiversity change issues. Since dark diversity is applicable to any taxonomic group, time period and global change driver, it can be a powerful tool to track global change effects simultaneously at local and regional levels, enhancing biodiversity change assessment, forecast, and nature conservation. To conclude, in this thesis I used both theoretical and practical approaches to assess both taxonomic and functional dark diversity in the context of global changes and obtained following main results, published in individual research papers. General principles how both observed and dark diversity would change over time (**I**), novel view how fast, how much and in what direction plant assemblages have changed over millennial time scales (**II**), and an overview how both dark diversity and functional traits can create windows of opportunities to protect or restore biodiversity (**III**).

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# SUMMARY IN ESTONIAN

## Tumeda elurikkuse dünaamika globaalmuutustes: taksonoomiline ja funktsionaalne perspektiiv

Globaalmuutused (nt. kliimatrendid ja teisenenud maakasutus) mõjutavad liikide levimist erinevate piirkondade vahel ja sees, ökoloogiliste koosluste moodustumist ja liikide omavahelisi seoseid. Sageli reageerivad liigid keskkonnamuutustele viivitusega, mistõttu mingil alal vaadeldud liigid ja nende funktsionaalsed tunnused ei pruugi anda piisavat teavet ökosüsteemi ja selle toimimise kohta. Oma doktoritöös pakun välja, et globaalmuutuste mõjusid saab paremini mõista uurides ala tumedat elurikkust – liikide ja tunnuste kogumit, mis sellesse paika sobivad ja on võimelised sinna kohale jõudma, kuid ometi puuduvad. Vaadeldud ja tume elurikkus koos moodustavad elupaiga liigifondi, mis hõlmab kogu piirkonna taksonoomilisest ja funktsionaalsest mitmekesisusest vaid selle osa, mis on uuringukoha jaoks ökoloogiliselt sobiv. Kuigi tumeda elurikkuse kontseptsiooni on varasemalt kasutatud eluskoosluste uurimisel, ei olnud enne seda doktoritööd ükski uuring otseselt käsitlenud globaalmuutuste mõju tumeda elurikkuse dünaamikale. Oma töös näitan, kuidas tumeda elurikkuse abil saab paremini hinnata bioloogilise mitmekesisuse muutuseid ulatuslikel keskkonnagradientidel ja aastatuhandeid hõlmavatel ajaperioodidel.

Taksonoomiline tume elurikkus näitab, kui palju elukohta sobivatest liikidest on hetkel puudu. Funktsionaalseid tunnuseid lisades saame uurida, miks sobivad liigid puuduvad ning kuidas toimib liikide „filtreerimine” piirkondliku ja kohaliku skaala vahel. Lisaks üksikutele funktsionaalsetele tunnustele, saab uurida ka kombineeritud tunnuseid, mis moodustavad virtuaalse tunnusruumi. Eluskoosluste funktsionaalse vaadeldud elurikkuse saab määratleda kui tunnusruumi osa, mis on uuritavas kohas esindatud. Funktsionaalne tume elurikkus on see osa tunnusruumist, mis võiks teoreetiliselt olla lokaalselt esindatud, kuid mida olemasolevad liigid ei hõlma. Nii saab selgitada, kuivõrd suure funktsionaalse samaväärsusega on liigifondi koosseis.

Oma doktoritöös andsin teoreetilise ülevaate vaadeldud ja tumeda elurikkuse dünaamikast. Tuvastades piirkonda sobivate, kuid kohapeal puuduvate liikide ja tunnuste kogumi, seob tume elurikkus piirkondlikud ja kohalikud skaalad ning võimaldab arvutada, kui täielik on iga uuritav ala (selleks on kasutusel koosluse täielikkuse indeks). Võrreldes vaadeldud ja tumeda elurikkuse liigilist koosseisu teatud aja jooksul saame tuvastada lokaalse dünaamika (liigid „liiguvad“ vaadeldud ja tumeda elurikkuse vahel), samuti uute sobivate liikide saabumist või olemasolevate kadumist piirkonnast. Jälgides koosluse täielikkust pikema aja jooksul saab uurida liigifondi muutusi. Näiteks, kui vaadeldud ja tume elurikkus suurenevad, kuid tume pool suureneb rohkem ning kiiremini, siis väheneb koosluse täielikkus, mis omakorda tähendab, et rohkem liike muutub uurimispaiga jaoks sobivaks, kuid nad ei jõua sinna kohale.

Hinnang, kui palju, kui kiiresti ja mis suunas liigifondid muutuvad, võib anda olulist teavet, kuidas kliima ja maakasutuse muutused mõjutavad bioloogilist mitmekesisust erinevatel ruumilistel ja ajalistel skaaladel. Funktsionaalsed tunnused aitavad välja selgitada põhjused, miks osad liigid ei jõua sobivatesse elupaikadesse, ja see teadmine on abiks looduskaitse tõhustamisel. Näiteks saab tumeda elurikkuse abil jälgida piirkondlikult väljasuremisohus olevaid liike ja tunnuseid, koostada nimekirja erilist kaitset vajavatest liikidest või tuvastada liike ja funktsionaalseid rühmi, mis sobivad vaesunud ökosüsteemi ja mida saaks taastamisega tagasi tuua. Koosluse täielikkuse hindamise abil saab eristada alad, kus tähelepanu peaks olema ökoloogilisel taastamisel (madal täielikkus) või olemasolevate ökosüsteemide kaitsel (kõrge täielikkus). Madala täielikkusega alade jaoks on tumedas elurikkuses palju alale sobivaid liike ning oskusliku tegevusega saab aidata neil ka elupaika levida ja püsima jääda. Kõrge täielikkusega aladel on ümbritsevas piirkonnas vähem liike, mis võiksid kohalikke väljasuremisi korvata. Doktoritöös kasutasin teoreetilist ja empiirilist lähenemist, et testida, kuidas globaalmuutused võivad mõjutada nii taksonoomilist kui ka funktsionaalset vaadeldavat ja tumedat elurikkust ja kuidas kasutada seda teavet kliimamuutustest enimmõjutatud liikide kaitse tõhustamiseks.

Tume elurikkus pakub ka uusi võimalusi uurimaks antropotseeni eluskoosluste moodustumist ja sellega seotud bioloogilise mitmekesisuse muutuseid. Näiteks võimaldab see kirjeldada, mismoodi ja kui kiiresti võis toimuda liikide saabumine ja kadumine mingis piirkonnas. Nii saab eristada liikide „liikumist“ tumedast elurikkusest vaadeldud elurikkuse hulka (elurikkuse kohalik suurenemine) ja vastupidi – liigid võivad lokaalselt välja surra ehk „liikuda“ tumeda elurikkuse hulka (kohalik väljalangemine). Liigifondi tasandil saab tuvastada liike, mis osutusid keskkonnamuutuste tõttu sobimatuteks (liigifondist väljalangemine), ja neid, mis osutusid sobivateks, kuid ei suutnud veel uurimisala asustada (liigifondi suurenemine).

Ühe osana oma doktoritööst uurisin õietolmuproove järvede ja soode setetest ning kirjeldasin nende proovide abil ka tumedat elurikkust erinevatel ajaperioodidel. Holotseeni ajal lõid globaalsed muutused Põhja-Euroopas soodsamad tingimused paljudele taimeliikidele ning seeläbi suurenes nii vaadeldud kui ka tume elurikkus. Sellegipoolest püsis enamik regiooni levinud sobivatest taksonitest tumedas elurikkuses. See viitab ulatuslikule viivitusele taksonite geograafilise levila suurenemises. Näiteks pärast mandrijää taandumist (soojenev kliima) ja holotseeni lõpuosas (suurenev inimmõju, elupaikade lisandumine) ilmusid mitmed taksonid just tumedasse elurikkusesse ja nende jõudmiseks vaadeldud elurikkusesse kulus sajandeid. Lisaks uurisin taimede funktsionaalsete tunnuste abil, miks need taksonid olid tumedas elurikkuses ning mis põhjustas levila suurenemise viivitusi. Võrreldes vaadeldud ja tumeda elurikkuse funktsionaalsete tunnuste keskmisi väärtusi, leidsin, et levila laienemise viivitus oli enamasti seotud taksonite suure funktsionaalse sarnasusega tumedas elurikkuses, samuti nende piiratud levimisvõime ja stressitalumatusega. Seega, kuigi mitmed taksonid osutusid muutunud kasvukoha tingimustele sobivaks, pidid nad konkureerima hea levimisvõime ja stressitaluvusega taksonitega, mis olid juba hõivanud olemasolevad ökonišid.

Oma doktoritöös leidsin, et nii vaadeldud kui tumeda elurikkuse funktsionaalsete tunnuste uurimine on võtmetähtsusega, et mõista, kuidas erinevad liigid reageerivad globaalsetele muutustele ja millistele rühmadele tuleb looduskaitses keskenduda. Näiteks piki Alpide kõrgusgradienti koosnes samblike tume elurikkus enamasti liikidest, mis on kliimasoojenemise osas tundlikud ja millel on mutualistlikke suhteid. Samamoodi olid samblikud eriti ohustatud keskkonnagradiendi mõlemas äärmuses. Madalamatel kõrgustel (soojemates tingimustes) oli liigifondi suurus ja täielikkus madal, mis näitab, et prognoositud kliimasoojenemise leevendamiseks on vaja nii kiireid taastamis- kui ka pikaajalisi kaitsemeetmeid. Sellest lähtuvalt teen ettepaneku, et madalamatel kõrgustel peaks taastamistegevuse fookuses olema koorikja kasvuvormiga samblikud, kuna neid on sellistes tingimustes tumedas elurikkuses osakaalult rohkem. Jahedamates kohtades mäe tipus on rohkem vaja kaitsealaseid jõupingutusi, et vähendada suursamblike ja suguliselt paljunevate liikide kohaliku ja piirkondliku väljasuremist, kuna need liigid on tundlikud temperatuuri tõusule ning aeglasemad uute populatsioonide loomisel.

Ökoloogia üks keskseid küsimusi on mõista, kui kiiresti on kliimamuutused ja inimtegevus mõjutanud elurikkust minevikus ning kuidas võivad need mõjud toimida alanud antropotseenis. Doktoritöös kirjeldan tumeda elurikkuse kontseptsiooni kui suhteliselt uudse, paindliku ja informatiivse lähenemisviisi eeliseid bioloogilise mitmekesisuse dünaamika uurimisel. Kuna tumeda elurikkuse kontseptsioon on rakendatav kõigi taksonoomiliste rühmade, ajaperioodide ja globaalmuutuste mõjurite korral, võiks see olla oluline vahend globaalmuutuste uuringuteks korraga nii kohalikul kui piirkondlikul skaalal, parandades bioloogilise mitmekesisuse muutuste hindamist, prognoosi ja looduskaitse tulemuslikkust. Kokkuvõtvalt, kasutades doktoritöös nii teoreetilist kui ka empiirilist lähenemist uurimaks taksonoomilist ja funktsionaalset tumedat elurikkust globaalmuutuste kontekstis, sain järgmised peamised tulemused, mis on avaldatud üksikuuringutes: üldpõhimõtted, kuidas nii vaadeldud kui ka tume elurikkus ajas muutuvad (**I**), uudne kirjeldus, kui kiiresti, kui palju ja mis suunas on taimekooslused aastatuhandete jooksul muutunud (**II**) ning ülevaade, kuidas nii tume elurikkus kui ka funktsionaalsed tunnused võivad luua uudseid võimalusi bioloogilise mitmekesisuse kaitsmisel ja taastamisel (**III**).

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Usually, doing a PhD is not an easy task. Doing a PhD in a foreign country, parenting a small kid, and facing a pandemic in between should be more than enough to make this task quite challenging. However, when you have support from an outstanding workgroup, family and friends, things get a lot easier. That said, I start by expressing my gratitude to my supervisor Meelis Pärtel for the whole intellectual support, guidance and inspiration during these years, and for always putting family and well-being as first priorities. I also thank my co-supervisor Carlos Pérez Carmona for accepting joining me in this journey and for always being there when I needed, showing how simple both coding and ecology could be (even though, most of the time, they aren't). Apart from supervisors, I would like to thank my wife Jéssica for being a source of inspiration and resilience, as well as for the whole support and encouragement given during these years. I also thank my daughter Laura for enchanting and intriguing me with her sharpness and curiosity, always wondering what papers I was working on and creating legendary quotes such as: "Dad, you are not a scientist, you don't explode things, you just make new figures", or "explaining why those species are more abundant is so easy, either they produce more seeds or people plant them more often". A special thanks to my parents and brother for their love and encouragement throughout my life, always supporting all my dreams and decisions. Also, thanks to my workgroup for the friendly and supportive environment. Thank you Riin, Kersti, Madli, Aurèle, Juni, Bruno, Eleonora, Enrico, Elisabeth, Slendy, and Guille et al. Last but not least, I thank my friend Michele for our coding/writing/drinking meetings in Kampa, making Czech Republic even more enjoyable, and my dear friends Jhonny, Katy, Leo, Kaisa, Thaisa, Miguel, Henri and Natalia for all good moments, making Estonian winter way easier to cope with. Thank you all!

***

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# PUBLICATIONS

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**Trindade, Diego P. F.**; Carmona, Carlos P.; Reitalu, Triin; Pärtel, Meelis (2023). Observed and dark diversity dynamics over millennial time scales: fast life-history traits linked to expansion lags of plants in northern Europe. Proceedings of the Royal Society B Biological Sciences, 290 (1990), 20221904. DOI: 10.1098/rspb.2022.1904.

Souza de Paula, Alexandre; Sfair, Julia C.; **Trindade, Diego P. F.**; Rito, Katia F.; Tabarelli, Marcelo; Barros, Maria F. (2023). The role of seed rain and soil seed bank in the regeneration of a Caatinga dry forest following slash-and-burn agriculture. Journal of Arid Environments, 211.
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Mugnai, Michele; **Trindade, Diego P. F.**; Thierry, Mélanie; Kaushik, Krishan; Hrček, Jan; Götzenberger, Lars (2022). Environment and space drive the community assembly of Atlantic European grasslands: Insights from multiple facets. Journal of Biogeography, 1−13. DOI: 10.1111/jbi.14331.

Pinho, Bruno X.; **Trindade, Diego P. F.**; Peres, Carlos A.; Jamelli, Davi; de Lima, Renato A. F.; Ribeiro, Elaine M. S.; Melo, Felipe P. L.; Leal, Inara R.; Tabarelli, Marcelo (2022). Cross-scale drivers of woody plant species commonness and rarity in the Brazilian drylands. Diversity and Distributions, 1497−1511. DOI: 10.1111/ddi.13587.

**Trindade, Diego P. F.**; Pärtel, Meelis; Carmona, Carlos Perez; Randlane, Tiina; Nascimbene, Juri (2021). Integrating dark diversity and functional traits to enhance nature conservation of epiphytic lichens: a case study from Northern Italy. Biodiversity and Conservation. DOI: 10.1007/s10531-021-02211-w.

**Trindade, Diego P. F.**; Carmona, Carlos P.; Pärtel, Meelis (2020). Temporal lags in observed and dark diversity in the Anthropocene. Global Change Biology, 26 (6), 3193−3201. DOI: 10.1111/gcb.15093.

**Trindade, Diego P. F**.; Sfair, Julia Caram; de Paula, Alexandre Souza; Barros, Maria Fabiola; Tabarelli, Marcelo (2020). Water availability mediates functional shifts across ontogenetic stages in a regenerating seasonally dry tropical forest. Journal of Vegetation Science. DOI: 10.1111/jvs.12896.

Luz-Freire, Hévila P.; **Trindade, Diego P. F**.; Sá-Neto, Raymundo J.; Corrêa, Michele M. (2014) Survival dynamics of Melocactus conoideus Buining & Brederoo (Cactaceae), a threatened species endemic to northeastern Brazil. Acta Botanica Brasilica 28: 293–297.

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| 2019 | Dora Plus activity 1.2 “PhD student mobility” scholarship to study at the University of South Bohemia, Czech Republic |
| 2019 | Dora Plus activity 1.1 grant (short study visits) to participate at the 6th Young Natural History Scientists Meeting in Paris, France. |

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**Trindade, Diego P. F.**; Carmona, Carlos P.; Reitalu, Triin; Pärtel, Meelis (2023). Observed and dark diversity dynamics over millennial time scales: fast life-history traits linked to expansion lags of plants in northern Europe. Proceedings of the Royal Society B Biological Sciences, 290 (1990), 20221904. DOI: 10.1098/rspb.2022.1904.

Souza de Paula, Alexandre; Sfair, Julia C.; **Trindade, Diego P. F.**; Rito, Katia F.; Tabarelli, Marcelo; Barros, Maria F. (2023). The role of seed rain and soil seed bank in the regeneration of a Caatinga dry forest following slash-and-burn agriculture. Journal of Arid Environments, 211.
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Mugnai, Michele; **Trindade, Diego P. F.**; Thierry, Mélanie; Kaushik, Krishan; Hrček, Jan; Götzenberger, Lars (2022). Environment and space drive the community assembly of Atlantic European grasslands: Insights from multiple facets. Journal of Biogeography, 1−13. DOI: 10.1111/jbi.14331.

Pinho, Bruno X.; **Trindade, Diego P. F.**; Peres, Carlos A.; Jamelli, Davi; de Lima, Renato A. F.; Ribeiro, Elaine M. S.; Melo, Felipe P. L.; Leal, Inara R.; Tabarelli, Marcelo (2022). Cross-scale drivers of woody plant species commonness and rarity in the Brazilian drylands. Diversity and Distributions, 1497−1511. DOI: 10.1111/ddi.13587.

**Trindade, Diego P. F.**; Pärtel, Meelis; Carmona, Carlos Perez; Randlane, Tiina; Nascimbene, Juri (2021). Integrating dark diversity and functional traits to enhance nature conservation of epiphytic lichens: a case study from Northern Italy. Biodiversity and Conservation. DOI: 10.1007/s10531-021-02211-w.

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**Trindade, Diego P. F**.; Sfair, Julia Caram; de Paula, Alexandre Souza; Barros, Maria Fabiola; Tabarelli, Marcelo (2020). Water availability mediates functional shifts across ontogenetic stages in a regenerating seasonally dry tropical forest. Journal of Vegetation Science. DOI: 10.1111/jvs.12896.

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## Õppetöö

### Ökoloogiliste koosluste andmeanalüüs (3 EAP)

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