

BRUNO PAGANELI

Dark diversity methods
for prioritization of areas and
species in nature conservation



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UNIVERSITY OF TARTU

Press

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Epigraph

I present a poetic summary of human interventions in nature (a central topic of the thesis), proposing education to mitigate current impacts. The poem, originally in Portuguese, features an acrostic on “biodiversidade”, with adjustments to preserve it in English (“biodiversity”).

Educar para a biodiversidade conservar

*Biodiversidade não é algo meramente atual, é fruto de longa história evolutiva,
Incomparável, sem par, sem individual prerrogativa.
O nosso dever, sem atraso adicional, é preservar e dela cuidar,
Diante disso, a próxima geração também dela poderá desfrutar.*

*Intrinseca é sua beleza, mas muitos não entendem sua importância,
Valorizam, em detrimento da biodiversidade, nossa relativa grandeza e ganância.
Educação e conscientização são o que urgentemente devemos compartilhar,
Revelando que a biodiversidade, na verdade, é a nossa própria vida a pulsar.*

*Sob uma urbanização intensa e consumo desenfreado,
Isso nos põe à beira do colapso, cujo limite já foi até calculado.
De toda forma, não podemos aceitar tal destino,
Afinal, temos esperança, a qual hoje chamamos de menina e menino.*

*Devemos agir com coragem e sabedoria,
E assim garantir que a biodiversidade floresça, dia após dia.
Permitindo não só que ela seja conservada,
Mas que permaneça sendo constantemente aprimorada.*

*Cuidemos das águas, das florestas, do ar,
Para que todas as formas de vida prossigam a prosperar.
Com a união de esforços, haverá mais esperança,
Só assim a biodiversidade continuará a ser nossa mais poderosa herança.*

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Translation into English

Education for biodiversity conservation

*Biodiversity is not a simple snapshot; it is the result of a long evolutionary history,
Incomparable, without peer, for many, a complete mystery,
Our duty, without further delay, is to preserve and take care of it,
Doing so, the next generation will also be able to enjoy it.*

*Its beauty is intrinsic, but many do not understand its importance,
Valuing, to the detriment of biodiversity, our relative greatness and widespread arrogance.
Education and awareness are what we urgently need to keep spreading,
Revealing that biodiversity, in fact, is our own life pulsating.*

*Suffering under intense urbanization and unchecked consumption,
Indisputably, we find ourselves on the brink of collapse, a limit already under calculation.
Though we cannot accept such a fate to be decreed,
Yet, we have hope, which today, we call ecologically educated kids.*

*We must act with courage and wisdom,
And thus, ensure that biodiversity flourishes with complete freedom
Allowing not only its conservation,
But its continuous progress and thriving transformation*

*Let's take care of water, forests, and air,
So that all forms of life can continue to thrive and bear.
By uniting our efforts, hope will grow above the average,
Only then will biodiversity remain our most powerful heritage.*

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LIST OF PUBLICATIONS

This thesis includes three published papers and one manuscript, all referenced throughout the text using Roman numerals as follows:

- I:** Paganeli, B., Fujinuma, J., Trindade, D.P.F., Carmona, C.P., Pärtel, M. (2024) “A Roadmap to Carefully Select Methods for Dark-Diversity Studies.” *Journal of Vegetation Science*, 35, e13264.
- II:** Riibak, K., Noreika, N., Helm, A., Öpik, M., Kook, E., Kasari-Toussaint, L., Jõks, Paganeli, P., Zárate Martínez, O., Tullus, H., Tullus, T., Lutter, R., Oja, E., Saag, A., Randlane, T., Pärtel, M. (2024) “Plants, Fungi, and Carabid Beetles in Temperate Forests: Both Observed and Dark Diversity Depend on Habitat Availability in Space and Time.” *Landscape Ecology* 39, 158.
- III:** Paganeli, P., Toussaint, A., Bueno, C.G., Fujinuma, J., Reier, Ü., Pärtel, M. (2022) “Dark Diversity at Home Describes the Success of Cross-Continent Tree Invasions.” *Diversity and Distributions*, 28, 1202–1213.
- IV:** Paganeli, B., Tordoni, E., Seebens, H., Pärtel, M. “Observed and Dark Diversity of Alien Plants Across the World” (manuscript).

Author Contributions to Publications. Key: Was responsible for (***) , Substantial contribution (**), or Minor contribution (*).

	Conceptualization	Data analysis	Interpretation and writing
Paper I	**	*	***
Paper II	**	*	*
Paper III	***	***	***
Paper IV	***	**	***

INTRODUCTION

1. HUMAN ACTIONS ON NATURE: IMPACTS AND STRATEGIES TO PREVENT FURTHER DAMAGES

Humans have become key components of nature whose ecological behavior has been reshaping landscapes and biodiversity, leading to consequences on both local and global scales (Currie et al. 2023, Ruggiero et al. 2022, Yuan et al. 2024). While conservation and restoration practices offer some benefits to ecosystems, most human-driven activities harm biodiversity (Ellis et al. 2012). Among these activities is the transformation of natural habitats into disturbed ones, potentially leading to the conversion of natural landscapes into anthropogenic ecosystems that can amplify the translocation of species beyond their natural dispersal ranges (Lorenzo & Morais 2023, Ruas et al., 2022). Transformation, disturbance and invasion of habitats are accelerating that can exclude native species either immediately or with a delay, escalating the threat to native biodiversity and ecosystem functioning worldwide (Kuussaari et al. 2009, Seebens et al. 2021). Understanding how habitat loss impacts biodiversity, alongside identifying the intensity and areas of future invasions, is crucial for preventing species losses, maintaining ecosystem function, and setting priority areas and species for conservation.

A possible strategy to enhance our understanding regarding future invasions relies on using the dark diversity concept, which refers to species ecologically suited to a site but currently absent (Pärtel et al., 2011). These absences are ecologically important, as they may indicate that local extinctions have occurred, the site is difficult to colonize, or it has just become suitable for a new species yet absent. By defining non-native dark diversity size and composition, we can identify the intensity of the threat likely to be faced by different areas and the identities of the species that pose that potential threat. Further, species traits can be assessed to infer why species are in dark diversity and the mechanisms causing species loss and vulnerability. Dark diversity within the nature conservation framework helps anticipate biodiversity loss in contexts of fragmented habitats and invasion, offering a proactive, ecologically and financially cost-effective way to counteract the current biodiversity crisis.

1.1 Dark Diversity: absent portion of the community's potential

Dark diversity has strong links with the community assembly theory. In a region with multiple species, environmental (resources such as soil nutrients and conditions such as temperature) and biotic filtering (species interactions) processes define which species tolerate the local ecological conditions (Zobel 2015). These filters narrow down the set of species found in the surrounding region, assembling

the site-specific species pool, which consists of regionally present species that fit their ecological requirements to a local area. Accordingly, during the filtering process, some species can successfully overcome the dispersal, environmental, and biotic filters from the region to the local site and be locally present (observed diversity). As a counterpart of the observed diversity, the part of the site-specific species pool that is absent forms the dark diversity of the studied area (Pärtel et al., 2011). Understanding why species are absent from suitable areas helps understand what is driving the community assembly process. However, since the species in dark diversity are locally absent, we cannot directly observe them. Instead, we rely on estimations to characterize the size and composition of the dark diversity (Carmona & Pärtel 2021). Thus, although many researchers agree on the usefulness of dark diversity, some see pitfalls when addressing method selection and reliability due to its unobservable nature (Hostens et al. 2023). While framing the dark diversity concept induced the development of new estimation methods (Carmona & Pärtel 2021), techniques to estimate site-specific species pools, such as Ellenberg numbers (Pärtel et al. 1996) and the Beals index (Ewald 2002), had already been in use much earlier. Available methods can be based on expert opinion (de Bello et al. 2016), analyses of matches between species' niches and site characteristics (Ronk et al. 2016), or information about patterns of species co-occurrence (Carmona & Pärtel 2021, Lewis et al. 2017). However, the most suitable estimating method can shift depending on the research goal and available information (Carmona & Pärtel 2021). Therefore, an overview is needed to evaluate the strengths and weaknesses of different approaches.

1.2 Dark diversity as a characteristic of study areas

The dark diversity concept has been widely applied in explorations of ecological communities (Fløjgaard et al., 2020), their functional properties (Morel et al., 2021, Trindade et al., 2023), and also separately across various taxonomic groups (Fernandes et al., 2019, Boussarie et al., 2018, Trindade et al., 2021, Valdez et al., 2021). This concept is particularly useful in guiding conservation efforts in contexts of human disturbances (Lewis et al., 2017, Moeslund et al., 2017), offering valuable information to address the challenges of fragmented landscapes. For example, temperate forests, historically converted into agricultural lands, have been abandoned, creating opportunities for tree species to recolonize. However, despite that process, old-growth forests continue to decline (Ceccherini et al. 2020, McDowell et al. 2020). While old-growth forests provide refuge for forest specialist species, their isolation within fragmented habitats reduces connectivity and might lead to higher dark diversity. Corresponding patterns have been found in grassland studies where fragmentation occurred similarly to those of old-growth forests due to abandonment of traditional management (Riibak et al. 2015, Prangel et al. 2023). In fragmented ecosystems, the availability and configuration of surrounding habitats play a crucial role in determining potential source areas

for recolonization. Even when conditions at the focal area are suitable, dispersal from these source areas can be slow, a phenomenon contributing to what is known as colonization credit (Rumpf et al. 2019). This delay in species recovery may be less noticeable in smaller, localized studies but becomes more evident across broader spatial dimensions (Jackson & Fahrig 2015). By assessing temporal scales, we can observe how historical landscape patterns remain correlated with current community composition, as the system might not have fully adapted to the changed habitats and landscape, influencing community assembly over time (Helm et al. 2006, Kuussaari et al. 2009, Mollier et al. 2022). Additionally, even in natural areas, many suitable species might be absent, and dark diversity tends to be much larger than the observed diversity (Riibak et al. 2015) and potentially more sensitive to ecosystem changes. Therefore, assessing the biodiversity potential of old-growth forests would benefit from a spatiotemporal analysis that considers the influence of surrounding habitats on both observed and dark diversity.

Although globalization has facilitated human movement between distant areas, many potential non-native species have not yet been dispersed and established (Essl et al. 2010). In this context, including potential invaders for consideration can reveal overlooked yet critical aspects of threats from non-native species (Ronk et al. 2017). Focusing on the dark diversity of non-native species provides valuable insights into an area's proneness to receiving additional non-native species, which is essential for effective conservation strategies. When we can identify key drivers of this process, such as replacing native vegetation with urbanized centers and infrastructure development (Boscutti et al. 2022), nature conservation actions can be better targeted. For example, examine the effect of new roads, which not only fragment habitats and limit species movement but paradoxically accelerate the spread of non-native species by creating new dispersal routes. These infrastructures make areas more suitable for non-native species, which initially contribute to the non-native dark diversity of the area, while observed diversity is not reacting immediately. High levels of urbanization, amplified by dense human populations and increased Gross Domestic Product, might further enhance conditions for non-native species spread by intensifying the chances of propagule pressure (Boscutti et al. 2022, Sharma et al. 2010). How these human-related changes in our world affect invasion on a global scale remains to be studied.

1.3 Dark diversity giving insights into why suitable species are absent

Dark diversity, containing species absent from suitable sites, can provide valuable insights to guide conservation strategies to prevent species loss. For biodiversity restoration, this framework reveals potential species to recolonize areas if local extinctions have happened due, for example, low stress or disturbance tolerance, insufficient resource acquisition, or dispersal limitations (Paganeli & Batalha

2022, Riibak et al. 2015, Trindade et al. 2020). By examining the identities and functional traits of suitable absent species, we gain insights into ecological reasons promoting their absences, allowing us to infer mechanisms behind species' absence and thereby inform strategies for enhancing biodiversity conservation.

Dark diversity can provide insights into which species have the potential to become more successful non-native species. For instance, increased chances of establishment and spread have been linked to traits related to efficient growth (Lamarque et al. 2011). Moreover, non-native species with successful establishment in new ranges need time to spread out, making the residence time a good proxy for introduction extent (Brendel et al. 2020). In general, species which are successful in their home range are likely more capable invaders as well. Among native range characteristics, range size has been particularly effective in predicting species performance in non-native areas (Díaz et al. 2023, Pyšek et al. 2009). This approach states that widespread species have a broad fundamental niche and an increased likelihood of being ecologically suitable in more non-native areas as well. However, many plant species are not yet present in suitable native sites, which can underestimate their invasion potential under the observed diversity framework (Svenning et al. 2008). Thus, dark diversity can handle that issue by defining the ecological suitability of absent species within home ranges, representing the niche breadth more holistically. Another complementary metric in our framework is the dark diversity probability (Moussund et al. 2017), an approach related to niche realization chances. Dark diversity probability accounts for how often a focal species fails to colonize suitable communities. Species displaying large cumulative ecological suitability and lower dark diversity probability as natives would theoretically perform better as non-natives.

2. AIMS

In this thesis, my general aim is to explore how dark diversity concept can be used to prioritize areas and species in nature conservation, making it more efficient. To achieve this goal, I have defined three specific aims:

1. To evaluate the performance of different dark diversity methods using theoretical considerations and empirical data (**I, IV**).
2. To explore the dark diversity size in studied areas across multiple scales (**I, II, and IV**) in order to: detail the area characteristics that influence their dark diversity size (**I, IV**); assess the effects of habitat availability in surrounding areas on local sites' biodiversity (**II**); and compare the current and potential future intensity of plant invasion in worldwide areas (**IV**).
3. To test if species with certain traits are more likely to be part of dark diversity (**I, II, III**); and if dark diversity-related metrics can better describe species invasiveness than a similar metric based on observed diversity (**III**).

A general scheme is displayed in Figure 1 to clarify how the three thesis aims are interconnected and linked to each paper, illustrating the spatial scales covered by the individual studies.

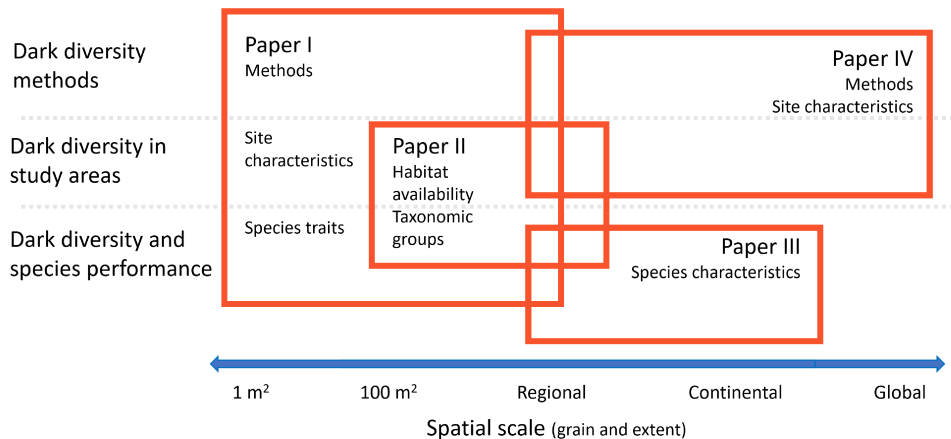


Figure 1. Schematic visualization of the thesis' aims and the themes covered in the papers. Paper **I** explores tundra vegetation in Northern Sweden. Paper **II** investigates multiple forests in Estonia. Paper **III** examines non-native tree species exchanged between Europe along with the Mediterranean Basin, and North America. Paper **IV** studies the potential future spread of thousands of recognized non-native vascular plant species worldwide.

3. METHODS

3.1 Dark diversity methods

The investigation conducted here operates within a macroecological framework. Accordingly, my colleagues and I explored various areas and plant communities using several datasets to address my objectives.

To evaluate dark diversity methods theoretically, I compiled a mini-review based on all available methodological papers on the topic (paper **I**). In a broad sense, a dark diversity method should sort species found in the surrounding area but absent from a site into those suitable for the site (i.e. belong to dark diversity) and those not suitable. In recent years, suitability has been used probabilistically where absent species belong to dark diversity with a certain probability (fuzzy set concept). I described the dark diversity methods that have been proposed, their strengths and weaknesses, and whether any of them stand out as having a better overall performance.

To assess the performance of selected methods with a particular dataset, we compare their ecological suitability estimation outcomes for both present and absent species (papers **I** and **IV**). A well-performing method should consistently assign high suitabilities for present species while varying suitabilities for absent species (some of them are likely in dark diversity, others are not). In paper **I**, we compared dark diversity estimations from two families of methods, niche-based and co-occurrence. For the former, I performed species distribution modeling built on general linear models (GLM). For the latter, **I** used two methods: the Beals index (Beals 1984, Cantanhêde et al. 2022) and the relatively recent hypergeometric method (Carmona & Pärtel 2021). The principle of the hypergeometric is that species that co-occur very often share ecological demands. We assess that through the areas-species matrix (areas can include countries, vegetation plots, or some other sample units). We can find how often various species pairwise co-occur and compare this with the random expectation, mathematically described by the hypergeometric distribution. This can be seen as an indication matrix if the differences between observed and expected co-occurrences are standardized (standardized effect sizes). We can use all present species in all areas to obtain their average indication of suitability for all other species, including present species, which allows us to test how well the method works. Steps of the hypergeometric methods are described in Figure 2. In paper **IV** involving non-native species globally, dark diversity scores for each species were grouped into two categories: for areas where the species was present as non-native and those where it was absent but suitable. We calculated the median value of scores for the two abovementioned groups of areas. We then used a Wilcoxon test to compare the median scores between the two groups.

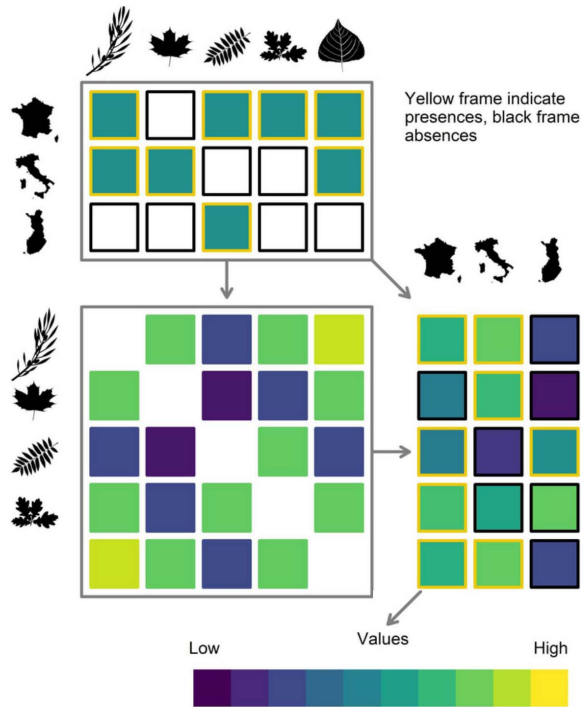


Figure 2. A conceptual scheme of the hypergeometric co-occurrence-based dark diversity estimation method. The upper left matrix contains the species occurrence data (rows: areas, columns: species). At the bottom left is the suitability indication matrix of species (whether two species co-occur more or less frequently than expected randomly). The bottom right matrix displays the average suitability indication of the present species to all other species in each area. Modified figure from paper III.

For papers I, II, and III, we calculated dark diversity through the hypergeometric method using the ‘DarkDiv’ package in R. For paper IV, involving a vast number of species, we developed a custom function in R instead of using the DarkDiv package. This function still relies on co-occurrence patterns (using only the native range of candidate non-native species) and the hypergeometric distribution to define their suitabilities. After defining the species’ ecological suitabilities, we rescaled all of them between +1 and –1 and maintained the potential new incursions only species with positive values on the list. Dark diversity size was estimated in each study area by summing suitabilities (dark diversity scores) of all absent species. Paper III focused on species rather than area, and we estimated two parameters related to the dark diversity for each species. Firstly, we calculated the sum of suitabilities across all study areas within the species’ native range, unforeseen whether the species was present or absent (dark diversity). The second parameter was the dark diversity probability, indicating how often the species are absent from ecologically suitable native areas (Moeslund et al. 2017). These metrics were compared with the native range size (number of areas where species was found).

3.2 The characteristics of study areas linked to dark diversity

To address the second specific aim, data across various spatial scales were used. The analysis goes from small-grain (sample unit sizes ranging from $1\text{ m} \times 1\text{ m}$ to $10\text{ m} \times 10\text{ m}$ in papers **I** and **II**) to larger grains (regional scales in papers **III** and **IV**). The study spans multiple extents (overall study area size), from local areas (**I**, **II**) passing to continental (**III**) and reaching a global extent (**IV**).

In paper **I**, we used data from Hostens and colleagues as a working example (2023). Their work used data from the Scandinavian subarctic mountains in Sweden, comprising 73 sites of $1\text{ m} \times 1\text{ m}$ and 34 sites of $10\text{ m} \times 10\text{ m}$. To explore the performance of different dark diversity methods, we calculated the dark diversity size of each site (summing all probabilities of suitable but absent species). In addition, to test which site characteristics make it more likely to have suitable species absent, we applied the dark diversity affinity approach (Fujinuma & Pärtel, 2023). This approach jointly evaluates the affinity of sites to keep suitable species absent (explored in the area-related sections of this thesis) and species' tendency to be likely in dark diversity (see more below in the species-related section). To get dark diversity estimates from the species distribution modeling test, we used climate and environmental information obtained from CHELSA version 1.2 (Karger et al., 2017), SoilTemp database (Lembrechts et al. 2020), and Copernicus Land Monitoring Service version 1.1 (European Union 2021). Here, I focus on two site characteristics related to human influences: its proximity to car roads and the proportion of bare soil, hereafter called disturbance proxy.

For paper **II**, exploring 100 boreo-nemoral old-growth forests in Estonia (Noreika et al. 2019), we found dark diversity for three functional groups of forest vegetation (woody species, ground layer and epiphytes). We related observed and dark diversity to forest availability in various spatial and temporal scales using generalized additive models (GAMs). To estimate the availability of forest habitats in the past and present, we used topographic maps from the 1900s, 1930s, 1970s, and 2010s. The spatial scale of that analysis goes from a radius of 0.5 km, 1 km, 2 km, to 5 km around each forest. Historical maps were digitized with a resolution of $100\text{ m} \times 100\text{ m}$, and the forest availability (forest cover proportion) was calculated for each time period. Forest availability was lowest at the start of the 20th century and has increased over the last 60 years since trees invaded a considerable share of abandoned agricultural lands. To find which spatial and temporal scale has the strongest effect on current observed or dark diversity, we compared 16 models where spatial and temporal scales were combined (auto-correlation prevents the inclusion of different scales into a single model). The best model was then selected based on the Akaike information criterion. We used bootstrapping with 95% confidence intervals to compare R^2 values between models for observed and dark diversity. Non-overlapping confidence intervals indicated a significant difference in response to the independent variables.

For paper **IV**, a global-scale approach was used to examine the potential new incursions of non-native species and the currently established ones, analyzing 367 botanical countries (Brummitt et al. 2001). We used more than 346000 vascular plant species distributions available on the Plants of the World database, including the status of nativeness. Using co-occurrences as native species, we estimated for each area the suitability of 11,699 vascular plant species that have been recorded as non-native at least once (showing the ability to invade). Using the non-native species richness data from the Plants of the World database, we compared current and future invasion trends by applying a Pearson correlation between non-native dark diversity size and non-native species richness. We explored the drivers of biological invasions through Random Forest modeling, linking both observed and dark diversity of non-native species to socioeconomic invasion drivers: gross domestic product and urbanization data from Wang & Sun (2022) and Chen et al. (2022), respectively.

3.3 The characteristics of species linked to dark diversity

In paper **I**, the tundra vegetation dataset included 49 plant species, including trees, shrubs, herbaceous, and grasses from tundra vegetation. Exploring the dark diversity affinity of species (Fujinuma & Pärtel, 2023), I investigate the influence of three functional traits (mycorrhizal type, seed mass, and plant height) on the species' affinity of composing the dark diversity in suitable sites. In addition, for each species, the nativeness index was calculated using the dynamics of records over time, as formulated by Hosten et al. (2023).

Although paper **II** on Estonian forest ecosystems also studied soil biota and carabid beetles, in my thesis, I focus on vegetation biodiversity described by three functional groups: woody plants (shrubs and trees: 35 species), ground vegetation (herbaceous vascular plants and dwarf shrubs: 115 species), and epiphytes (bryophytes: 80 species; lichens: 202 species). The literature suggests that these groups may display different requirements regarding forest availability in their surroundings (Pan et al. 2022), and comparison of diversity patterns across group will also give information on respective species.

In paper **III**, exploring tree species in Europe with the Mediterranean basin and North-America, I aimed to test whether dark diversity-related metrics at the native range better explain species invasiveness compared to an observed diversity metric. To achieve this, two sets of models were defined: one using dark diversity-related metrics, proxy for niche width (sum of location suitabilities) and realization chances (dark diversity probability), and the other using an observed diversity measure (number of locations where the focal species was recorded). Data on species occurrences in North America were obtained from the USDA Plants Database (2020), while data for Europe and the Mediterranean Basin were sourced from the GlobalTreeSearch database (Beech et al., 2017). Species status (native or non-native) was determined using the Global Naturalized Alien Flora database (van Kleunen et al., 2019). We studied 81 tree species whose status was

defined as native in North America and non-native in Europe with the Mediterranean Basin, and 89 species displaying the opposite status in those areas. Our dependent variable was always the invasion success (number of locations occupied at the non-native ranges). The independent variables included metrics calculated from native ranges. Model either included two dark diversity-related metrics or one based on observed diversity. All models included as additional independent variables some essential functional traits (here I examine just leaf nitrogen content, retrieved from the TRY Plant Trait Database – Kattge et al., 2020) and information on their approximate residence time (obtained from various sources). The comparison of the models obtained was made using the Akaike criterium information.

4. RESULTS

4.1 Dark diversity methods: an overview and tests with empirical data

Here, I provide an overview of the most commonly used methods to estimate dark diversity, summarizing their strengths and weaknesses. I also highlight some findings from studies that compare the outputs of these methods.

Among the most straightforward methods to estimate dark diversity is the expert opinion. It uses specialist descriptions about how likely a given species could live in a site where it is absent. However, in investigations dealing with small grain sizes or some underexplored areas, scientists with that information are often unavailable (de Bello et al. 2016). An alternative approach consists of sampling the same habitat type in the surrounding region to define the list of surveyed species that are absent in a given site, which would be the area's dark diversity (Jiménez-Alfaro et al. 2018). As nature is a continuous rather than a clear categorical measure, that strategy might bias the dark diversity estimation by erroneously defining the site-specific species pool.

Another family of methods is the use of matches between sites, resources and conditions, and species niches. For this purpose, Ellenberg indicator values (Ellenberg et al. 1991) were often used (Pärtel et al. 1996). Multiple databases can offer those data, but they are limited by geographical and taxonomic scope, resolution, and uncertainties in how to weigh different gradients. A more direct approach is species distribution modeling, which predicts species' presences based on ecological resources and conditions. Species distribution modeling is common in large-scale studies, where abiotic factors are usually readily available from various environmental maps. However, for smaller grain studies such as vegetation plot scale, those data are often unavailable, making neighboring plots be treated as similar or even identical. That method is also biased by species frequency on the dataset, where widespread species tend to obtain higher dark diversity values, and rare species are likely to get lower values. However, favorability correction (Real et al. 2006) can make the probabilities independent of species frequency.

Co-occurrence-based dark diversity methods offer advantages over previous approaches by not requiring expert input, species databases, or environmental data. These methods use the idea that co-occurring species share abiotic and biotic preferences, allowing present species to indicate suitability for absent ones. A potential issue in this group of methods might be the inclusion of successional sites with transient species compositions and geographical variation in co-occurrence patterns. The Beals index has been commonly used, but it tends to overestimate suitabilities for common species and underestimate rare ones. This bias can be corrected by specifying thresholds (Lewis et al. 2015), which can be considered arbitrary. Alternatively, the additional step of applying a favorability correction to the Beals index is also possible.

The hypergeometric method is another co-occurrence-based method that defines dark diversity with a probabilistic output (Carmona & Pärtel 2021). That method compares the candidate alien species' co-occurrence frequencies with the frequency expected by random chance (null model), determined by the hypergeometric distribution mean and standard deviation. The obtained suitability is mathematically independent of the regional frequencies of species. For example, if a species is very common, it co-occurs with many other species, but the same is expected randomly. If the observed and random patterns do not differ, there will not be a positive indication from this common species. Similarly, if the co-occurrence of two species in an area is due to contrasting habitats happening side-by-side, it is not likely to have the same pattern in other areas. Thus, such random co-occurrences do not give a strong signal.

In the two datasets where we analyzed the performance of dark diversity estimations, our tests corroborate the abovementioned statements about the hypergeometric method. In Figure 3c and d, it is well seen that the hypergeometric method provided more differentiated suitabilities for species when they were present (usually higher values) or absent (values spanning across the suitability gradient). It was evident at small grain sizes (1 square meter and 100 square meters – Figure 3a, e.g., *Linnaea borealis*, *Luzula multiflora*) and also in larger areas (“botanical countries” – Figure 3b). Beals and niche-based methods did not display a very accurate estimate of dark diversity for individual species by reproducing suitabilities of sites where the species compose the observed diversity to sites where it was in part of the dark diversity (e.g., *Empetrum nigrum*, *Salix lanata* – Figure 3a).

Our Wilcoxon test applied in the paper IV data, where we aimed to compare the median scores between the areas where the species were present (hypothesized higher suitabilities) and areas where they were part of the dark diversity (hypothesized more varying but often smaller suitabilities), was statistically significant (p-value < 0.0001), confirming the good performance of the hypergeometric method at larger grain sizes.

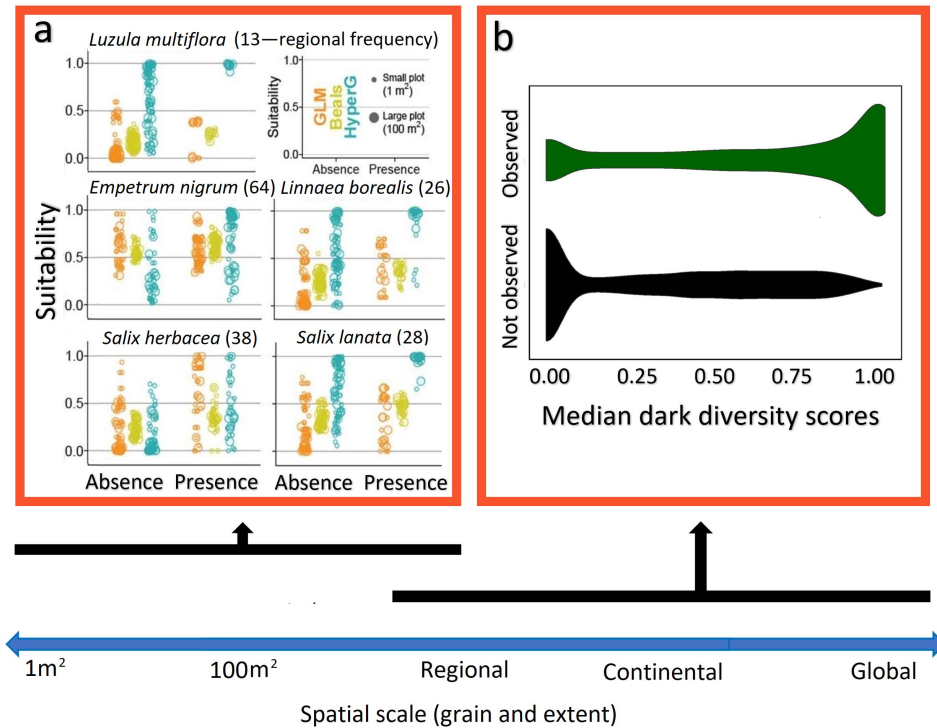


Figure 3. Methods comparison based on probabilistic species suitability across different spatial scales. Paper I results are labeled as panel a, and paper IV in panel b. In panel a, I show a comparative analysis of three methods defining the species' suitability for tundra vegetation plots depending on whether studied species are present or absent. Panel b displays the median dark diversity scores (proxies for suitabilities) of non-native species in areas where they have been established (green) and areas where they remain absent (black). This figure combines elements from figures in papers I and IV.

4.2 Dark diversity describing study areas in various contexts

By exploring the factors influencing dark diversity size, we applied the concept across various conservation contexts and using many area characteristics. In paper I, our results suggested that sites in tundra vegetation near roads and displaying intense disturbances *in situ* tend to display a higher likelihood to include their suitable species in the dark diversity (Figure 4a). The analysis from paper II (Figure 4b) shows that woody species were not statistically significantly influenced by forest availability. In turn, the observed diversity of ground vegetation increased significantly with a higher forest availability. Similarly, dark diversity was lower in plots where old-growth forests were historically widely available. Similarly to ground vegetation, observed and dark diversity of epiphytes responded oppositely to forest availability: while observed diversity increased, dark diversity decreased. The analysis of R^2 values shows that dark diversity is more strongly related to forest availability (R^2 95% confidence range 0.47– 0.72)

compared to observed diversity (0.13–0.40), making it more informative in assessing the effects of forest availability in the surroundings on the local biodiversity.

The non-native species richness and non-native dark diversity size in 367 areas worldwide were negatively correlated (Spearman’s $\rho = -0.27$, $p < 0.001$). Thus, our results suggest that the current and potential future invasion intensity tend not to overlap, and heavily invaded areas tend to be less prone to receive additional non-native species (Figure 4c). The Gross Domestic Product of areas influenced their invasion richness and non-native dark diversity in a contrasting manner. While richer economies tend to be more invaded, they simultaneously have a lower tendency to receive additional non-native species (Figure 4c). Instead, urbanization level had a very similar effect on our two non-native biodiversity metrics, where highly urbanized areas have a higher tendency to display the largest non-native species pool (large non-native species richness and larger non-native dark diversity – Figure 4c).

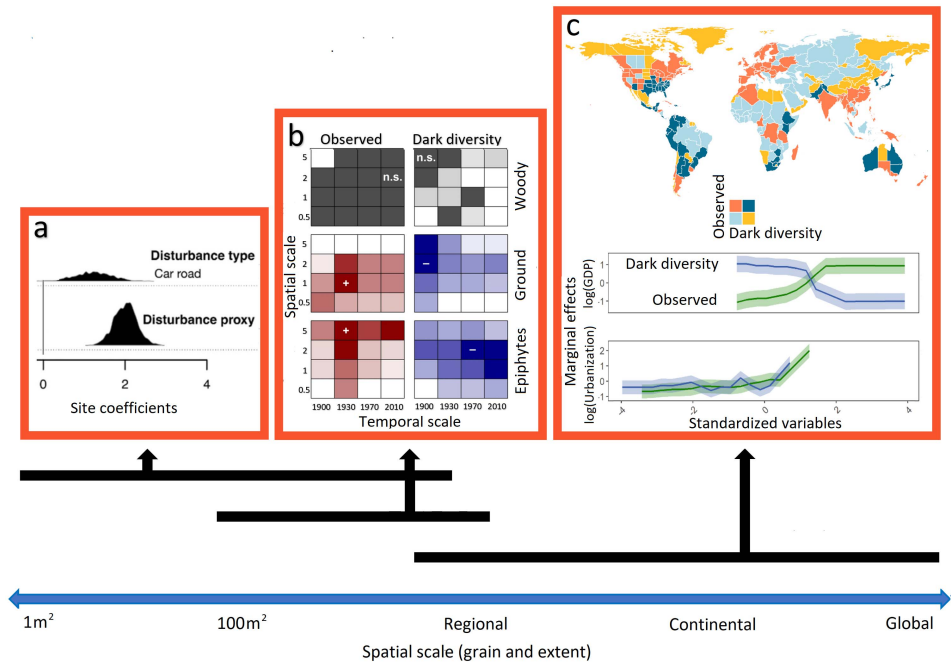


Figure 4. Approaches to explore observed and dark diversity in study areas of various spatial scales. While the results of paper I appear in panel a, those from paper II are in panel b, and paper IV is shown in panel c. Panel a displays the coefficients of the dark diversity affinity model for areas, positively coefficients demonstrating the tendency of respective areas tend to have suitable species in their dark diversity. Panel b shows relationships among spatial and temporal scale on biodiversity metrics, with red indicating positive, blue negative, and grey as non-significant (n.s.). The best models are marked with the sign. Non-native species richness and dark non-native diversity size are split above and below the median, indicated by a color scheme in panel c, where the random forest output is also shown below the map. This figure is based on modified figures from papers I, II, and IV.

4.3 Species characteristics related to dark diversity

Species characteristics influenced their chances of being in dark diversity. In the tundra vegetation study, the dark diversity affinity of species revealed that tall species with small seeds and all mycorrhizal types, except ErM, were more likely to be part of the dark diversity (Figure 5a). The nativeness index, however, did not significantly influence the likelihood of a species being in dark diversity. My hypothesis in paper III was corroborated since our species-related hypothesis showed that dark diversity-related metrics estimated at the native range describe tree species invasiveness better than an observed diversity-related metric (Figure 5b). Specifically, the overall best-performing model used dark diversity and displayed a delta AIC of 0.00 and an R^2 of 0.43. In contrast, the top model based on observed diversity obtained a delta AIC of 5.39 with an R^2 of 0.39. As expected, species with higher dark diversity probability at their home range were less successful as non-native. In turn, species displaying more suitable locations at their native range were also more successful in their invaded range. However, the trend was not symmetrical; the number of suitable locations had a positive effect on tree species invasiveness native to Europe and invading North America, and not vice versa. Leaf nitrogen content and residence time were positively correlated to invasion success (Fig. 5b).

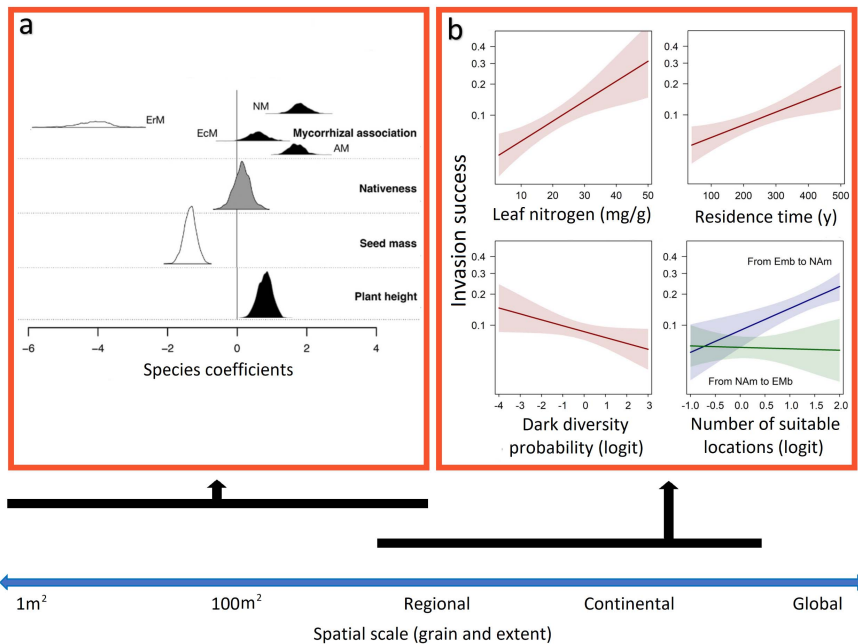


Figure 5. Approaches to explore species-related characteristics linked to dark diversity. Paper I is labeled as panel a, and paper III as panel b. Panel a displays the dark diversity affinity coefficients of species; significant positive coefficients show that species such traits are mre likely in dark diversity (colored in black), significant negative coefficients show the opposite tendency (in white); non-significant coefficients are in grey. Panel b displays how invasion success of tree species are related to species characteristics; the number of suitable locations showed a relationship only for invasions from Europe with the Mediterranean Basin to North America.

5. DISCUSSION

The investigations conducted in this thesis demonstrate how dark diversity can be used as a powerful and reliable tool to address significant challenges for nature conservation. Dark diversity should be estimated as it is directly unobservable. My findings show that methods have significantly evolved since the concept was framed. The hypergeometric method, which relies on species co-occurrences, proves to be highly effective and straightforward in its data requirements. To further illustrate this evolution, the papers in this thesis discuss dark diversity across a broad range of scales in different ecological contexts, from habitat fragmentation to the introduction of non-native species. The combination of these investigations reveals critical information to help prevent biodiversity loss and forecast potential invasion events even before they occur. This approach offers a valuable tool for nature conservation in addressing components of the ongoing biodiversity crisis and prioritizing key areas and species for action.

5.1 The hypergeometric method provides reliable estimates of dark diversity

The results from papers **I** and **IV** confirmed that the hypergeometric method is a well-performing dark diversity estimation method, and for the studied datasets, it is currently the most reliable framework. As shown in paper **I**, alternatives as Beals, another co-occurrence-based method, and species distribution modeling exhibit weaker performance than the hypergeometric method. The hypergeometric method displays higher suitabilities for present species and varying (usually lower) suitability for absent species, as a given area might be more suitable for some absent species but likely unsuitable for many. In general, in tundra vegetation explored on a small grain scale (**I**), distribution modelling and Beals replicate the suitability of sites where the species are present to sites where the species is a candidate for dark diversity (Fig. 3). This approach contradicts the dark diversity definition proposed by Pärtel et al. (2011). According to this definition, dark diversity refers to the ecological suitability or habitat suitability (sometimes referred to as the beta niche or Grinnellian niche, Grinnell 1917) of a species at a specific focal area. Although the hypergeometric method performs well in multiple contexts (papers **I**, **II**, **III**, **IV**), in certain situations, present species can be ecologically scored with lower suitability (Fig. 3a). However, those scenarios do not necessarily contradict what is expected in a well-performing method (**I**, **IV**). This may occur due to environmental changes such as habitat disturbance, where previously suitable sites become less suitable over time, leading to the potential displacement of established species (Paganeli et al. 2020, Trindade et al. 2020). Additionally, these “unsuitable” species may indicate a transient establishment during extreme weather events, when species that would not typically survive are temporarily present. Although methods inevitably simplify real-world complexities, I argue

that co-occurrence patterns also capture broader ecological fits, such as species' microclimate and soil preferences (papers **I**, **IV**), all through indirect evidence (co-occurrence patterns). Meanwhile, I expect that the advancement of techniques such as machine learning (Koger 2020), ordinations (Brown et al., 2019), or joint species distribution modeling based on Bayesian statistics (Ovaskainen et al., 2016) could further enhance dark diversity estimations.

5.2 Study area characteristics describing absences of dark diversity species

Paper **I**, which explores tundra vegetation, showed that anthropically disturbed areas have a higher affinity to reduce their biodiversity potential (Figure 4c, paper **I**). The test assessing the disturbance proxy was highly significant, indicating that sites with higher disturbances tend to have more ecologically suitable species as components of the sites' dark diversity. Similarly, sites closer to roads exhibit significantly fewer species than the site could theoretically host. These findings align with what we expected, highlighting the substantial negative impact of human activities on biodiversity (Boscutti et al. 2022, Hou et al. 2023). While these sites remain suitable for the dark diversity species, continued expansion of human-altered landscapes may lead to the loss of some of these species, first by making those sites unsuitable and removing them from the site-specific species pool, and, in more severe cases, removing them from the regional species pool (Trindade et al. 2020).

Results from paper **II**, which focused on Estonian old-growth forests, suggest that woody species, ground vegetation, and epiphytes respond differently to the availability of forest in their surroundings. This finding highlights the importance of considering functional groups' specific habitat preferences in conservation planning. Woody species did not show a statistically significant relationship with forest availability, suggesting that their dark diversity size remains relatively stable despite varying forest availability. This stability may indicate that woody species possess greater resilience to habitat fragmentation, possibly due to their longer lifespans or higher persistence abilities (Szitar et al. 2023). In addition, most woody species in Estonia can grow relatively well in open landscapes, and a few tree species usually dominate dense forests. In contrast to woody species, ground vegetation showed that forest availability in the surroundings significantly affects both its observed and dark diversity. However, this effect on observed diversity peaked at intermediate levels of forest availability, indicating that while ground vegetation benefits from forest connectivity, excessive forest cover may limit the light and resources available to support diverse ground-layer species (Moola & Vasseur 2008). Additionally, sites displaying a historically high forest availability tend to have a larger number of absent yet suitable ground vegetation species, reinforcing the importance of historical continuity to improve ecological suitability for these communities (Fritz et al. 2008, Mollier et al. 2022). Epiphytes showed

a slightly different trend than ground vegetation, requiring forest availability at a larger spatial scale, even though their dark diversity was similarly negatively correlated with forest availability. This pattern indicates that epiphytes are highly sensitive to forest fragmentation and rely on well-connected habitats to fit their ecological requirements (Fritz et al. 2008). The contrasting responses among these groups and their respective biodiversity metrics emphasize the need for a multifaceted conservation approach that maintains a mosaic of forest habitats, allowing communities to come closer to their full biodiversity potential. Our tests also indicated that dark diversity was more sensitive to forest availability surrounding our studied forest plots than observed diversity. This can be understood by the size of dark diversity, which is typically much larger than observed diversity (Riibak et al. 2015). This characteristic further confirms our suggestion regarding using both biodiversity metrics, dark and observed diversity, to gain a more holistic view of status and trends in local diversity.

Human activities not only tend to exclude native species but can also drive the arrival of mostly unwanted species, the non-natives (Hulme 2021). Our global study (paper IV) suggested that humans affect the ecological suitability and presence of non-native species worldwide. The results indicate that urbanization is more linked to the creation of suitable habitats for non-native species, as it positively affects both observed and non-native dark diversity. However, while urbanization influences the suitability of an area for non-native species, one of the main factors that explains how these suitabilities are realized is the gross domestic product (IV). While economically rich areas tend to display higher non-native species richness, areas in economic development tend to include their set of ecologically suitable non-native species in the dark diversity. These findings align with biological invasion theory, as the gross domestic product can serve as a proxy for intense human movement and higher trade intensity, triggering the exchange of a larger number of non-native species (Hulme 2021).

By mapping non-native dark diversity, we show the first global study describing the proneness of areas to receive additional non-native plant species. Our results suggest that areas in Europe, Asia, and Africa have already been exposed to a large set of ecologically suitable non-native species. Thus, the non-native dark diversity is somewhat lower than in other areas in the World. Historically, Eurasian areas have served as hubs for trade and colonization, activities linked with high propagule pressure that has facilitated the arrival of the largest fraction of their non-native species pool (including many established archaeophytes, with long residence time – Lenzner et al. 2022, van Kleunen et al. 2015). This seems at odds with a previous study that suggested an intensive influx of non-native species should hit Europe (Seebens et al. 2021). Our metric, however, does not consider propagule pressure as Seebens and colleagues (2021) did. I concur that propagule pressure remains high in this economically rich and globally influential continent. Nonetheless, our focus is on ecological suitability instead of propagule pressure. Despite the potential for a massive number of species to continue arriving, only a small fraction of those not yet present may be suitable. Likewise, in the Northern Hemisphere, coastal areas exhibit smaller non-native dark

diversity sizes. This distribution pattern of dark diversity in these areas could be attributed to the historically intense movement of people and trade along ocean borders (Hou 2015). As expected, such activities are associated with the significant reduction of dispersal barriers, thereby increasing propagule pressure and the realization of ecologically suitable invasions (IV). Although our metric suggests these areas are not highly prone to additional non-native species arrivals, it is important to recognize the role of the observed portion of non-native diversity already established. Thus, the potential arrival of relatively few non-native species in these areas should not be underestimated, as their capacity to become invasive and trigger ecological damage demands vigilance.

The study from a global perspective (IV) revealed that many areas worldwide show a higher potential for receiving additional non-native species, making them a priority due to the potential larger new influx of such species. Mountainous areas along the Pacific and near the Himalayas exhibit high non-native dark diversity, likely due to geographic barriers that limit human movement and, consequently, the arrival of many ecologically suitable non-native species. I observed that tropical, economically rich areas, such as parts of Australia and Southeast Brazil, tend to host a higher number of non-native species and also possess large non-native dark diversity, making them home to some of the largest non-native species pools globally. Meanwhile, tropical areas in Africa, despite their naturally high biodiversity and potential to host multiple non-native species (Gaston & Blackburn 2000, Stohlgren et al. 2003), display relatively fewer observed non-native species but larger non-native dark diversity sizes. According to our results, this may be due to limited economic development, which restricts the realization of many ecologically suitable non-native species. Defining potential future invasions before they occur is a key goal in biological invasion studies (Fournier et al. 2019). When combined with other strategies, this approach could save trillions of dollars, which could then be redirected to meet other societal demands (Cuthbert et al. 2022).

5.3 Species characteristics describing their likelihood for dark diversity

In paper I, exploring tundra vegetation, the dark diversity affinity of species indicated which functional traits facilitate or hinder the establishment of suitable species. All mycorrhizal types, except for ErM, were associated with a higher chance of being in dark diversity, whereas ErM plants were less likely in dark diversity. As described by Hostens (et al. 2023), the area is dominated by ErM plants, which can perform as a well-connected meta-community where random local extinctions are rapidly compensated by recolonizations from numerous similar vegetation patches in the surroundings. Tall species were more likely in dark diversity, contrasting with observations from temperate vegetation (Fujinuma & Pärtel 2023). Because height can be linked to drought and cold sensitivity in

tundra vegetation (Olson et al. 2018), it is reasonable to expect taller plants to display lower persistence even in suitable sites. Suitable species with small seeds were more often absent. While seed size is commonly linked to dispersal (Riibak et al. 2015, 2017), in our study, it seems to be more linked with establishment likelihood, as dispersal may be less limiting in open tundra landscapes, especially because seedlings coming from large seeds have higher survival rates in dense vegetation (Moles & Westoby 2004). The nativeness index was the only species characteristic not associated with the chance of being in dark diversity. That result suggests a lack of invasion lag (a phase in the biological invasion process between the arrival and establishment of alien species – Coutts et al. 2018). That output is a positive message for conservation, suggesting that future invasions are unlikely. This finding aligns with the idea that plant communities in tundra generally exhibit high resistance to invasion (Eskelinen et al. 2017). Despite this, the intensification of anthropogenic activities has been linked to the range expansion of non-native plant species in Arctic areas (Bartlett et al. 2021). Therefore, the dark diversity of alien species serves as an early warning system for currently unlikely but potential future invasions. That framework offers valuable tools for developing conservation actions at both local and regional scales, which are crucial for more holistic ecosystem monitoring and nature conservation.

Our native range of dark diversity-related metrics offers an efficient tool for predicting and prioritizing species with higher invasion potential, addressing the challenge of mitigating biological invasions even before they occur. Studies suggest that species widespread in their native ranges often become the most widespread non-natives (Carboni et al., 2016; Fristoe et al., 2021). Traditional methods using expert-drawn maps can overestimate presence by including unsuitable areas or conversely underestimate species invasiveness by excluding suitable but unoccupied areas. Our dark diversity species-related metrics address these gaps by combining native location suitabilities (proxy of niche breadth) and dark diversity probability, which measures how often suitable areas remain unoccupied. Species with larger and frequently occupied suitable ranges are more likely to find similar conditions in non-native ranges, enhancing their chances of establishment if they happen to arrive. Additionally, traits like higher leaf nitrogen content, linked to more efficient growth, further boost invasion success (Lamarque et al., 2011). Our results show that our dark diversity-related metrics improve the prediction of species invasiveness, allowing the prioritization of species that should be more carefully assisted in order to avoid their introduction. This creates a window of opportunities to track and prevent the establishment of potentially invasive species before their arrival.

6. CONCLUSIONS

This thesis used the dark diversity concept to understand the effects of human interventions on nature and guide conservation actions by indicating areas and species priorities. I reached the following conclusions:

- (1) Based on the literature review, dark diversity methods based on species co-occurrences generally work best, especially the hypergeometric method. Through a series of empirical tests ranging from local to global scales, I got further support for the hypergeometric method which performed better than the alternatives. I conclude that the hypergeometric method is currently the more reliable method to estimate the size and composition of the dark diversity (**I, IV**).
- (2) Dark diversity analyses revealed the effect of human disturbances in local vegetation sites in tundra – disturbed sites lack more likely their suitable species (**I**). By exploring Estonian boreo-nemoral forests, I found that dark diversity can be a more efficient metric than observed diversity to detect the effects of forest availability on local communities. By compiling the first global map describing the intensity of potential but not yet realized plant invasions (**IV**), I showed that more potential invaders are for areas which are currently less invaded, and socioeconomic parameters can predict where future invasions are most likely.
- (3) I identified species characteristics linked to their chances of being in dark diversity. In tundra vegetation, these characteristics hint that persistence is more limiting than dispersal (**I**). Exploring the context of biological invasion, I found that dark diversity-related metrics calculated at species native range significantly improved the description of species invasiveness (**III**).

This thesis advances scientific understanding by setting the current most efficient dark diversity estimation method and integrating it into practical conservation efforts. My thesis highlights the need to adopt predictive conservation strategies to address the ongoing impacts of human-induced habitat degradation, disturbances, and the introduction of alien species, all actions linked to the intense worldwide biodiversity loss.

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SUMMARY IN ENGLISH

Human activities are increasingly reshaping natural ecosystems and introducing non-native species worldwide, accelerating to the current biodiversity crisis. Despite scientific advancements in nature conservation, new tools are extremely needed to better set priorities, identify adverse anthropogenic impacts and mitigate their effects. While observed diversity is a valuable indicator of the present vegetation state, it represents only a fraction of the site-specific species pool that determines the potential of the local biodiversity. A complementary and equally important metric is the unrealized part of that potential, the dark diversity – the set of species that can be reached and established in a currently unoccupied area. Dark diversity framework in conservation is the main topic of my thesis, hopefully helping to maintain healthy ecosystems.

Although dark diversity itself is a very compelling concept, it cannot be observed directly and, thus, should be studied through indirect methods. To reliably apply the dark diversity concept, its users should be confident about the effectiveness of selected methods for determining its size and composition. Based on literature review (paper **I**), I suggest the hypergeometric dark diversity estimation method, based on the analyses of species' co-occurrences. The philosophy of this method states that species that frequently co-occur together share ecological demands. The method compares the number of observed occurrences between two species with the random expectation, mathematically described by the hypergeometric distribution. If we know the patterns of species co-occurrences, we can use observed species to estimate which absent species are suitable for the studied site. The hypergeometric method benefits from some good properties – it only needs species co-occurrence data, and it estimates ecological suitabilities independent from species frequencies. The methodological testing in papers **I** and **IV** showed that the hypergeometric dark diversity method achieved the expected output. The strong support for the hypergeometric method outlines it as a highly recommended method for estimating dark diversity. In this thesis, I show how this method can be applied across various spatial scales and contexts, obtaining sound dark diversity estimations, from small-grain sites (1 m × 1 m and 10 m × 10 m) within a regional extent (papers **I** and **II**) to larger grains (e.g., “botanical countries”) at continental (**III**) and global extents (**IV**).

Using dark diversity size in studied areas, I explored how selected anthropogenic factors related to the current biodiversity crisis can influence species' absences. In paper **I**, exploring tundra vegetation, the dark diversity affinity was an excellent approach to describe how human disturbances at the landscape level decrease the presence of ecologically suitable species in study sites. In paper **II** about old-growth forests in Estonia, various spatial and temporal scales were investigated revealing how the availability of surrounding forests influenced biodiversity in 100 areas. The results suggested that dark diversity is more sensitive metric to forest availability than observed diversity, particularly for epiphytes. Given that observed diversity represents typically only a small fraction of the potential biodiversity, dark diversity proves to be an additional, sometimes

more effective, tool for detecting local extinctions. The paper **II** also showed that functional groups of vegetation (woody plants, ground vegetation, and epiphytes) have different spatial and temporal dependencies on forest availability in the surroundings. Overall, local forest biodiversity was typically higher in sites surrounded by ancient forests, in contrast to forests which appeared during the last century and which evidently not yet function as a part of biodiversity network. This result highlights the importance of preserving ancient forests in Estonia.

Another key aspect of my thesis was to integrate dark diversity into the research of non-native species. The biological invasion involves the introduction of new species through anthropogenic means, often threatening native biodiversity. Typically, invasion starts slowly, with a few individuals. Eradication of a non-native species then likely, while later it becomes often impossible. Consequently, an important task for biological invasion studies include predictions of potential non-native species even before their arrival. In papers **III** and **IV**, together with colleagues I explored this predictive strategy by applying the dark diversity concept to non-native species at continental or global extents. This strategy had never been implemented globally with such a large number of species (over 11,000 non-native vascular plants) prior to our work (**IV**). The dark diversity approach predicting potential new incursions might help preventing biodiversity loss and ecosystem service degradation. By comparing relationships of observed and dark diversity of non-native species with principal socio-economic factors, it was found that while highly urbanized areas create suitable habitats for non-native species (positive relationship with both metrics), economic power increases possibilities for suitable non-native species to arrive (positive relationship with observed diversity and negative with dark diversity). Globally the non-native species observed and dark diversities were negatively correlated. For example, while areas in Europe display the highest number of non-native plants, their dark diversity is relatively lower. Still, many areas are characterized by high non-native dark diversity, including higher latitudes in the Northern Hemisphere, Central Asia, Australia, and parts of North and South America. This information allows the arrival of non-native species to be anticipated, set priorities in the combat against them, and, thus, mitigate the effect of biological invasions by proactively implementing biologically and financially cost-effective conservation practices.

Dark diversity can give valuable information for studied species. Studying multiple species in tundra vegetation (**I**), I found that a higher chance to be in dark diversity is typical for taller plants with small seeds, forming other mycorrhizal types than the ericoid one. Based on this information, I could infer reasons why species might be absent from suitable habitats. Further exploring characteristics of tree species growing in Europe and the Mediterranean basin, or North America, I related their invasiveness with metrics calculated based on their native range (**III**). Invasiveness was more strongly related to metrics calculated from dark diversity (potential native range size and the proportion how much it was realized) than the so-far wide used observed native range size. Used dark diversity related metrics captured the ecological niche breadth, and its realization

likelihood. Thus, we can predict taxa which might have a high invasion potential. The proposed metrics could theoretically predict invasion even for species without a prior invasion history. Consequently, this framework can be used to identify species with higher invasion potential, helping prevent the spread of new non-native species globally.

My investigations demonstrate that dark diversity can significantly enhance conservation practices. In my thesis, I found that dark diversity methods are both feasible and reliable, and the hypergeometric method is among top performers. The use of dark diversity can assess threats to native biodiversity across various spatial scales and predict potential incursions of non-native species. This knowledge allows for more efficient nature conservation strategies, enabling proactive measures to prevent ecological threats such as biological invasions and declines in biodiversity due to habitat loss. This is especially important because restoration practices and post-invasion control often require considerable resources and time, and may not fully restore biodiversity to its initial state. The information produced in this thesis can serve as a benchmark in the field of biological invasions, being the first study to predict the future spread of the entire set of currently known non-native plant species globally, potentially saving trillions of dollars that could be reallocated to meet other societal needs. Integrating dark diversity into nature conservation offers new tools to better understand and proactively combat species loss in our increasingly fragmented and invaded ecosystems, from local to global scales.

SUMMARY IN ESTONIAN

Tumeda elurikkuse meetodid alade ja liikide looduskaitseliste prioriteetide määramiseks

Elurikkuse säilitamise õpetus

(vabatõlge autori portugali keelsest luuletusest „Educar para a biodiversidade conservar“)

*Elurikkus pole hetkepilt, vaid pika arenguloo vili,
Võrratu, ainulaadne, kuid paljudele mõistatuslikki.
Meie kohus, nüüd ja kohe, on seda hoida ja kaitsta,
Et ka järgmine põlvkond saaks selle hüvesid maitsta.*

*Selle ilu on sügav, kuid paljud ei mõista selle väärtust,
Nad hindavad elurikkuse arvelt ahnelt iseenda tähtsust.
Nüüd kiirelt jagama peame nii teadmisi kui mõistmist,
Näitama, et elurikkus on osa meie enda vereringest.*

*Tehiskeskkonnas, ohjeldamatu tarbimise uimas,
Leiame end hävingu äärelt, lagi on juba ulatuses.
Me ei saa sellise saatusega leppida,
Me lootuseks on lapsed, kes suudavad meid endid õpetada.*

*Peame tegutsema täie julguse ja tarkusega,
Ja nii tagama, et elurikkus saaks vabalt õitseda.
Et lisaks olemasoleva hoidmisele,
Oleks ruumi ka taastumisele ja täiustumisele.*

*Hoolitseme vee, metsade ja õhu eest,
Et elu kõik vormid saaksid edeneda veel.
Meie ühiste jõupingutustega kasvab lootus,
Jääb alles elurikkus, me võimsaim pärandus.*

Inimtegevus mõjutab üha enam looduslike ökosüsteeme – elupaigad killustuvad ning suureneb võõrliikide osakaal, mis omakorda süvendab käimasolevat elurikkuse kriisi. Vaatamata edusammudele looduskaitse korralduses, on teaduses vaja uusi teoreetilisi lähtekohti ja meetodikaid, et tuvastada looduskaitsele prioriteetseid alasid ja liike ning leevendada kahjulikke inimõjusid. Vaadeldud liigirikkus on väärtuslik mõõdik praeguse looduse seisundi hindamiseks, kuid see esindab vaid üht osa uurimisala eriomasest liigifondist ehk elurikkuse potentsiaalset. Sama oluline on uurida selle potentsiaali realiseerimata osa. Uurimisalalt

puuduv liigifondi osa on tume elurikkus – liikide kogum, mis võib teoreetiliselt uurimisalale levida ja seal püsima jääda. Ökosüsteemide vaesumine on üks tänapäeva keskkonnakriisi olulisemaid osasid. Tumeda elurikkuse käsitlus looduskaitstes on minu doktoritöö peamine teema, mis loodetavasti aitab kaasa hästi toimivate ökosüsteemide säilitamisele. Ma püstitasin kolm eesmärki. (1) Hinnata tumeda elurikkuse meetodite tõhusust nii kirjanduse kui ka andmete analüüsi alusel. (2) Selgitada, kuidas tumeda elurikkuse suurust on seotud uurimistalade mitmesuguste tunnustega ja elupaiga kättesaadavusega ümbruskonnas, ja kuidas on üleilmselt seotud võõrliikide vaadeldud ja tume elurikkus. (3) Testida, kas teatud omadustega liigid on suurema tõenäosusega tumedas elurikkuses ning kas tumeda elurikkuse abil leitud mõõdikud prognoosivad võõrliikide levikut paremini kui loodusliku levila suurus.

Kuigi tume elurikkus on iseenesest konkreetne mõiste, ei saa seda otseselt vaadelda ega mõõta, vaid tuleb piirduda kaudsete meetoditega. Tumeda elurikkuse käsitluse usaldusväärseks rakendamiseks peaksime olema kindlad valitud meetodite tõhususes selle suuruse ja liigilise koosseisu määramisel. Kirjanduse analüüsi tulemusena (artikkel **I**) soovitan hüpergeomeetrilist tumeda elurikkuse meetodit, mis seisneb liikide koosesinemiste uurimisel. See meetod põhineb eeldusel, et sageli koosesinevad liigid omavad sarnaseid ökoloogilisi nõudmisi. Meetod võrdleb leitud liigipaaride koosesinemiste hulka sellega, mida võiks juhuslikult eeldada. Viimast kirjeldab matemaatiliselt hüpergeomeetriline jaotus. Kui me teame piirkonnas olevate liikide koosesinemiste sagedusi, saame kasutada vaadeldud liike, et hinnata, millised puuduolevad liigid sobivad uuritavale alale. Hüpergeomeetrilisel meetodil on mitmed eeliseid – selle jaoks on vaja vaid liikide koosesinemise andmeid ja saadud ökoloogilise sobivuse hinnangud ei sõltu liikide sagedusest. Metoodika testimine artiklites **I** ja **IV** näitas, et hüpergeomeetriline tumeda elurikkuse meetodi kasutamine saavutas oodatud tulemuse. Oma doktoritöös kasutasin seda metoodikat erinevates looduskaitsetes küsimustes ja erinevates ruumiskaalades, saades usaldusväärseid tumeda elurikkuse hinnanguid alates väikestest vaatlusaladest (1 m × 1 m ja 10 m × 10 m) regionaalsel skaalal (artiklid **I**, ja **II**) kuni suuremate aladeni (nn „botaanilised riigid“) mandri (**III**) ja globaalsel skaalal (**IV**).

Kasutades tumeda elurikkuse hinnangut, uurisin, kuidas praeguse elurikkuse kriisiga seotud inimtegevuse erinevad tagajärjed võivad mõjutada taimeliikide puudumist. Tundra taimkatet käsitlevas artiklis **I** leidsime, et tumeda elurikkuse abil saab kirjeldada, kuidas inimtegevus maastikus vähendab ökoloogiliselt sobivate liikide jõudmist uuritud kooslustesse. Eesti vanu metsi käsitlevas artiklis **II** uurisime 100 proovialal, kuidas ümbritsev metsasus erinevatel ruumi- ja ajaskaaladel mõjutab elurikkust. Leidsime, et tume elurikkus on metsasuse suhtes tundlikum kui vaadeldud elurikkus, seda eriti epifüütide puhul. Kuna vaadeldud elurikkus on enamasti vaid väike osa potentsiaalsest elurikkusest, siis on tume elurikkus täiendavaks ja tõhusaks abinõuks kohalike väljasuremiste tuvastamisel. Artiklis **II** näitasime ka, et taimkatte funktsionaalsete rühmade (puittaimed, alustaimestik ja epifüüdid) elurikkuse seosed ümbritseva metsasusega kehtivad erinevatel ruumilistel ja ajalistel skaaladel. Üldreeglina on metsakoosluste-

elurikkus suurem nendel aladel, mida ümbritsevad pika ajalooga metsad, kuid viimase sajandi jooksul tekkinud metsad ei toimi veel elurikkuse võrgustiku osana. See tulemus toob esile vanade metsade säilitamise olulisuse Eestis.

Teine oluline aspekt minu doktoritöös oli tumeda elurikkuse kasutamine võõrliikide uuringutes. Bioloogiline invasioon on võõrliikide levimine inimtegevuse abil, mille tulemusena on looduslik elurikkus tihti ohustatud. Tavaliselt algab invasioon aeglaselt, väheste isenditega. Siis on võõrliigi kõrvaldamine tõenäoline, kuid hiljem muutub see sageli võimatuks. Seetõttu on bioloogilise invasiooni uuringute üheks oluliseks eesmärgiks prognoosida võimalikke võõrliike juba enne nende tegelikku saabumist. Artiklites **III** ja **IV** uurisime võõrliikide leviku prognoosimise võimalikkust, rakendades tumeda elurikkuse käsitlust mandri (Põhja-Ameerika, Euroopa) ja globaalsel skaalal. Sellist uute võõrliikide saabumist prognoosivat strateegiat ei olnud varem globaalselt nii paljudele liikidele korraga (üle 11 000 võimaliku soontaime võõrliigi) rakendatud. Tumeda elurikkuse käsitlus potentsiaalsete uute võõrliikide leidmiseks võimaldab ennetada elurikkuse kadu ja tagada ökosüsteemide toimimise. Võrreldes soontaime võõrliikide vaadeldud ja tumeda elurikkuse seoseid globaalsel skaalal, leidsime, et kuigi linnastunud alad loovad võõrliikidele sobivaid elupaiku (positiivne seos nii vaadeldud kui ka tumeda elurikkusega), siis majanduslik heaolu võimaldab sobilikel võõrliikidel ka kohale jõuda (positiivne seos vaadeldud elurikkusega ja negatiivne tumeda elurikkusega). Globaalsel skaalal on „botaaniliste riikide“ võõrliikide vaadeldud ja tume elurikkus negatiivselt korreleeritud. Näiteks, kuigi Euroopas on kõige rohkem võõrliike, siis on nende tume elurikkus ehk potentsiaal uute võõrliikide saabumiseks suhteliselt väike. Siiski on palju piirkondi, kus võõrliikide tume elurikkus on suur, näiteks kõrgemad laiuskraadid põhjapoolkeral, Kesk-Aasias, Austraalias ning mitmetes Põhja- ja Lõuna-Ameerika piirkondades. See teave võimaldab ennustada võõrliikide saabumist, seada prioriteete nende vastu võitlemiseks ja seega leevendada bioloogilise invasiooni mõju, rakendades ennetavalt bioloogiliselt ja rahaliselt kulutõhusamaid kaitsemeetmeid.

Tume elurikkus annab ka uuritavate liikide kohta olulist teavet. Uurides mitmeid liike tundrataimestikus (**I**), leidsime, et suurema tõenäosusega satuvad tumedasse elurikkusesse kõrgemakasvulised ja väikeste seemnetega taimed, kes moodustavad teisi mükoriisatüüpe kui erikoidne. Selle teabe abil saab luua hüpoteese, miks teatud liigid on sobivatest elupaikadest tihti puudu. Uurides puuliike, mida leidub kas Euroopas või Põhja-Ameerikas, seostasime nende invasiivsust loodusliku levila parameetritega (**III**). Võõrliigi invasioon oli tugevamini seotud tumeda elurikkuse abil leitud mõõdikutega (potentsiaalne looduslik levila suurus ja selle realiseerumise osakaal) kui siiani laialtkasutatud loodusliku levila suurusega. Tumedal elurikkusel põhinevad mõõdikud kirjeldasid ilmselt paremini liikide niši laiust ning andsid hinnangu nišipiirangule. Seega saab seda käsitlust kasutada liikide tuvastamiseks, millel on suur võimalus võõras kohas levida. Need uudsed mõõdikud võiksid teoreetiliselt prognoosida invasiivsust isegi neile liikidele, millel ei ole varasemat invasiioniajalugu, aidates nii ennetada uute võõrliikide levikut kõikjal maailmas.

Minu uuringu tulemused näitavad, et võttes arvesse ka tumedat elurikkust, saame oluliselt parandada looduskaitsepraktikaid. Oma doktoritöös näitasin, et tumeda elurikkuse meetodid on praktilised ja usaldusväärsed, ning hüpergeomeetriline meetod on hetkel olemasolevatest parim. Tumeda elurikkuse abil saab hinnata ohte elurikkusele erinevatel ruumiskaaladel ja ennustada võimalikke võõrliikide saabumisi. Võttes kasutusele ennetavaid meetmeid, et ära hoida ökoloogilisi ohte, nagu bioloogilised invasioonid ja elurikkuse vähenemine elupaikade kadumise tõttu, saame tõhustada looduskaitsestrateegiaid. See on eriti oluline, kuna elupaikade taastamine või juba invasiivsetest võõrliikidest lahtisaamine nõuavad sageli märkimisväärselt vahendeid ja aega ning looduslik elurikkus ei pruugi taastuda. Minu doktoritöös ennustati esimest korda kõigi praegu teadaolevate soontaimede võõrliikide levikut üle maailma, olles verstepost bioloogiliste invasioonide teadusharu valdkonnas. Tumeda elurikkuse kaasamine looduskaitseesse pakub uusi tööriistu, et paremini mõista ja ennetada liikide kadumist meie üha rohkem killustatud ja võõrliikidest mõjutatud ökosüsteemides, alates koosluse tasandilt kuni kogu planeedi ulatuseni.

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PUBLICATIONS

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Research articles:

- Riibak, K., Noreika, N., Helm, A., Öpik, M., Kook, E., Kasari-Toussaint, L., Jõks, M., **Paganeli, B.**, Zárate Martínez, O., Tullus, H., Tullus, T., Lutter, R., Oja, E., Saag, A., Randle, T., & Pärtel, M. (2024). Plants, fungi, and carabid beetles in temperate forests: both observed and dark diversity depend on habitat availability in space and time. *Landscape Ecology*.
<https://doi.org/10.1007/s10980-024-01960-7>
- Hábenczyus, A. A., Weiterová, I., Foremnik, K., Jakob, A., Khopkar, S., Kumar, A., Lazăr, A., **Paganeli, B.**, Samraoui, K.R., Sidwell, J., Hrček, J., Lepš, J., Segrestin, J. (2024) Long-term effects of meadow management on seed bank diversity and composition. *Journal of Vegetation Science*.
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- Paganeli, B.**, Fujinuma, J., Trindade, D.P.F., Carmona, C.P., Pärtel, M. (2024). A roadmap to carefully select methods for dark diversity studies. *Journal of Vegetation Science* <https://doi.org/10.1111/jvs.13264>
- Paganeli, B.**, Toussaint, A., Bueno, C. G., Fujinuma, J., Reier, Ü., & Pärtel, M. (2022). Dark diversity at home describes the success of cross-continent tree invasions. *Diversity and Distributions* <https://doi.org/10.1111/ddi.13522>
- Paganeli, B.**, & Batalha, M. A. (2022). Effects of nitrogen and phosphorus availability on the early growth of two congeneric pairs of savanna and forest species. *Brazilian Journal of Biology*.
<https://doi.org/10.1590/1519-6984.235573>
- Ruggiero, M. H., Bentos, A. B., **Paganeli, B.**, Adorno, H. A., Lorandi, R., Lollo, J. A. di, & Moschini, L. E. (2022). Determinação do potencial de contaminação de aquíferos no município de Artur Nogueira (São Paulo, Brasil), por meio de atributos geoambientais. *Cuadernos de Geografía*.
<https://doi.org/10.15446/rcdg.v31n2.88995>
- Paganeli, B.**, Dexter, K. G., & Batalha, M. A. (2020). Early growth in a congeneric pair of savanna and seasonal forest trees under different nitrogen and phosphorus availability. *Theoretical and Experimental Plant Physiology*.
<https://doi.org/10.1007/s40626-019-00164-8>

Books chapters:

- Paganeli, B.** (2024). Cerrado, cerradinho, cerradão: muita biodiversidade mermão! (English: Cerrado, cerradinho, cerradão: huge biodiversity!) ISBN: 978-989-37-8532-4.
- Paganeli, B.** (2024). Amor pandêmico. Três Quartos de um Amor. (English: Pandemic love. Three-Quarters of a Love), Vol. IV Chiado Books. ISBN: 978-989-37-7447-2.

Paganeli, B. (2023). Educação para a conservação da biodiversidade. Entre o sono e o sonho. (English: Education for biodiversity conservation. Between sleep and dream). Chiado Books. ISBN: 978-989-37-6386-5.

Valencio N., Ibrahim, S.Y., **Paganeli, B.** Santos, M.R. Gonçalves, J.C. et al. (2018) Inundações e cuidado integral: guia para discussões técnicas e comunitárias. ISBN: 978-65-88873-14-4.

Teaching:

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Environmental Science Teacher at the São Carlos municipal school. From Aug 2014 until Dec 2015.

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- 01.03.2017–12.10.2019 Magistriõpingud keskkonnateadustes, São Carlose föderaalne ülikool, Brasiilia.
- 16.10.2018–11.03.2019 Külalismagistrant, Edinburghi ülikool, Ühendkuningriik.
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Erialased toetused:

- Dora Plus osa 1.1, Leping 5.10-6.1/22/277-2, “Lühiajaline välisvisiit” (1406 €).
Juuni 2022.
- Dora Plus osa 1.2, Leping 5.10-6.1/21/170-2, “Pikaajaline välisvisiit” (4235 €).
Juuni 2021.
- FAPESP, Leping 2017/04937-8, stipendium (kokku 54412 R\$). Makstud iga-
kuiselt juulist 2017 kuni juunini 2019.
- BEPE–FAPESP 1.2, Leping 2018/11557-0, stipendium (4400 £). August 2018.
- Ciências sem fronteiras. Leping CsF 88888.021420/2013-00, taotlus: 11711,
stipendium (16252 €). Juuli 2013.

Auhinnad:

- 20.09.2024 66th Rahvusvahelise Taimkatteteaduse Ühingu (IAVS) 66.
Aastakonverntsil noore teadlase postri auhind, Funchal, Madeira,
Portugal.
- 28.10.2022 Teaduse tippkeskuse EcolChange lõpukonverntsil “Kolme
minuti ettekande” auhind, Tartu, Eesti.

Teadusartiklid:

- Riibak, K., Noreika, N., Helm, A., Öpik, M., Kook, E., Kasari-Toussaint, L., Jõks, M., **Paganeli, B.**, Zárate Martínez, O., Tullus, H., Tullus, T., Lutter, R., Oja, E., Saag, A., Randlane, T., & Pärtel, M. (2024). Plants, fungi, and carabid beetles in temperate forests: both observed and dark diversity depend on habitat availability in space and time. *Landscape Ecology*.
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- Hábenczyus, A. A., Weiterová, I., Foremnik, K., Jakob, A., Khopkar, S., Kumar, A., Lazăr, A., **Paganeli, B.**, Samraoui, K.R., Sidwell, J., Hrček, J., Lepš, J., Segrestin, J. (2024) Long-term effects of meadow management on seed bank diversity and composition. *Journal of Vegetation Science*.
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- Paganeli, B.**, Fujinuma, J., Trindade, D.P.F., Carmona, C.P., Pärtel, M. (2024). A roadmap to carefully select methods for dark diversity studies. *Journal of Vegetation Science* <https://doi.org/10.1111/jvs.13264>
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- Ruggiero, M. H., Bentos, A. B., **Paganeli, B.**, Adorno, H. A., Lorandi, R., Lollo, J. A. di, & Moschini, L. E. (2022). Determinação do potencial de contaminação de aquíferos no município de Artur Nogueira (São Paulo, Brasil), por meio de atributos geoambientais. *Cuadernos de Geografía*.
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- Paganeli, B.**, Dexter, K. G., & Batalha, M. A. (2020). Early growth in a congeneric pair of savanna and seasonal forest trees under different nitrogen and phosphorus availability. *Theoretical and Experimental Plant Physiology*
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Raamatupeatükid:

- Paganeli, B.** (2024). *Cerrado, cerradinho, cerradão: muita biodiversidade mermão!* ISBN: 978-989-37-8532-4.
- Paganeli, B.** (2024). *Amor pandêmico. Três Quartos de um Amor. Vol. IV* Chiado Books. ISBN: 978-989-37-7447-2.
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Õppetöö:

Õppeassistent professor Marco Batalha bakalaureusekursuses “**Koosluste ökoloogia II**”, São Carlose föderaalne ülikool, veebruar – juuli 2016.

Õppeassistent prof. Dr. Evelise Nunes Fragoso de Moura ja Maria da Graça Melão bakalaureusekursustes “**Tsütoloogia**”, “**Histoloogia**” ja “**Embrüoloogia**”, São Carlose föderaalne ülikool.

Keskkonnateaduste õpetaja São Carlose linnakoolis, august 2014 – detsember 2015.

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