

ARGO RONK

Plant diversity patterns across Europe:
observed and dark diversity



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UNIVERSITY OF TARTU
Press

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Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in botany and mycology at the University of Tartu on May 16, 2016 by the Scientific Council of the Institute of Ecology and Earth Sciences University of Tartu.

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Commencement: Council hall of the University of Tartu, 18 Ülikooli Street, Tartu, on September 15, 2016 at 10.15 a.m.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu

ISSN 1024-6479

ISBN 978-9949-77-206-3 (print)

ISBN 978-9949-77-207-0 (pdf)

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University of Tartu Press

www.tyk.ee

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications denoted in the text by Roman numerals:

- I. Ronk, A., Szava-Kovats, R. & Pärtel, M. (2015) Applying the dark diversity concept to plants at the European scale. *Ecography*, 38, 1015-1025
- II. Ronk, A.; de Bello, F.; Fibich, P.; Pärtel, M. (2016) Large-scale dark diversity estimates: new perspectives with combined methods. *Ecology and Evolution*, doi:10.1002/ece3.2371
- III. Ronk, A.; Szava-Kovats, R.C.; Zobel, M.; Pärtel, M. Observed and dark diversity of alien plant species in Europe: estimating future invasion risk. *Biodiversity and Conservation*, Conditionally accepted.
- IV. Lewis, R.J., de Bello, F., Bennett, J.A., Fibich, P., Finerty, G.E., Götzenberger, L., Hiiesalu, I., Kasari, L., Lepš, J., Májecková, M., Mudrák, O., Riibak, K., Ronk, A., Rychtecká, T., Vítová, A. & Pärtel, M. (2016) Applying the dark diversity concept to nature conservation. *Conservation Biology*, doi: 10.1111/cobi.12723.
- V. Kalwij, J.M., Robertson, M.P., Ronk, A., Zobel, M. & Pärtel, M. (2014) Spatially-Explicit Estimation of Geographical Representation in Large-Scale Species Distribution Datasets. *Plos One*, 9, e85306.

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Author's contribution to the publications:

- I. had the main responsibility to develop the idea, data collection and analysis as well as manuscript preparation
- II. participated in developing the idea, had the main responsibility in data collection and analysis as well as manuscript preparation
- III. participated in developing the idea, had the main responsibility in data collection and analysis as well as manuscript preparation
- IV. participated in the workshop developing the idea and manuscript preparation
- V. participated in data collection and manuscript preparation

INTRODUCTION

Biodiversity and especially large numbers of species found in a study area have drawn the attention of ecologists and conservationists for decades (Gaston, 2000; Barthlott *et al.*, 2007). Species richness as a diversity metric has been used in plethora of studies, for example, to quantify local biodiversity (Wilson *et al.*, 2012) and determining biodiversity hotspots (Myers *et al.*, 2000), testing ecological “rules” (e.g. species-area relationships, latitudinal gradient) (Lomolino, 2000; Hawkins *et al.*, 2003; Hillebrand, 2004), or in nature conservation for delineating areas for conservation (Kerr, 1997; Myers *et al.*, 2000). It is estimated that globally total vascular plant species richness varies around 300 000 species, but the actual knowledge of how species are distributed is heavily lacking, a phenomenon known as the Wallace shortfall (Whittaker *et al.*, 2005; Bini *et al.*, 2006; Lomolino *et al.*, 2006). Even in Europe, which has a long history of botanical research and is one of the most well studied continents globally, only ca. 20% of the plant species is actually mapped in grids based at the continental scale (Keil *et al.*, 2012; Kalwij *et al.*, 2014). In the era of such shortfall, biodiversity studies could be made more informative by looking at observed species richness in a broader perspective than study site itself. Does exploring species absences, more specifically the absent but suitable species for a site, has generally not been known.

Variation in large scale species richness patterns is caused by different natural and anthropogenic factors. For example, it has been found that species richness of most taxonomic groups declines from the equator to the poles (Hawkins *et al.*, 2003). Although the underlying mechanisms behind this relationship are not unambiguously clear (Hillebrand, 2004), this latitudinal gradient is often explained by the energy hypothesis (Hawkins *et al.*, 2003), i.e., that at higher latitudes species distributions is mostly limited by harsh temperatures. It has been found that climate is a driving factor for shaping large scale species richness patterns (Thuiller *et al.*, 2005a; Bucklin *et al.*, 2015). However, at the European scale, it has been suggested that in some cases dispersal limitation of the species can be an even stronger factor than climate (Svenning & Skov, 2005). Species have not yet fulfilled all the climatically suitable areas in Europe since the last glaciation (Svenning & Skov, 2004). Anthropogenic factors additionally shape species distribution patterns. Humans can influence distribution patterns by altering the landscape structure, for example, by intensity of agriculture, or acting as a dispersal vector for species (Pyšek *et al.*, 2005; Kowarik, 2011; Bellard *et al.*, 2013). Nevertheless, climate is the main mechanism determining current species diversity patterns and it has been emphasized that at the European scale in the face of the climate change most species will considerably change their current geographical ranges (Bakkenes, 2002; Araújo *et al.*, 2011). It has been also found that climate change could also promote the relative importance of alien species in local floras due to increased environmental suitability (Bellard *et al.*, 2013).

The species pool concept states that variation in local diversity is dependent on the availability of species from a larger area (Cornell & Harrison, 2014; Zobel, 2016). A species pool is defined as all species from the surroundings that are able to inhabit a particular site (Pärtel *et al.*, 1996; Zobel *et al.*, 1998; Pärtel *et al.*, 2011). In the current work, species pool is considered “filtered”, i.e., that all the species in the species pool must be able to disperse to the study site and tolerate local environmental conditions. Species in the species pool can be divided into two groups: species which are already present at the site (observed species richness) and species which are absent from the site but are also suitable (dark diversity). Dark diversity is defined as species that are currently absent from the study site but that are potentially able to disperse there and be able to tolerate the local environmental conditions in at least some part of the study site (Pärtel *et al.*, 2011, 2013; Ronk *et al.*, 2015; Lewis *et al.*, 2016a). In order to estimate dark diversity we first need to explore species distributions in the study area and determine their environmental preferences. The dark diversity concept is related only to “filtered” (site- or habitat-specific) species pool (Pärtel *et al.*, 2011; Ronk *et al.*, 2015). In order to estimate site specific species pool and hence dark diversity (absent part of species pool), the species must be able to pervade a series of filters: a geographical filter (able to disperse to study site) and an environmental filter (tolerate the local environmental conditions) (Zobel, 1997). The geographical filter is based on some geographical constraint, for example, we can delimit the area where we could assume that species can potentially disperse to our study site (Graves & Gotelli, 1983; Finnie *et al.*, 2007). The environmental filter is based on species environmental preferences.

Although dark diversity cannot be sampled directly as opposed to observed species richness, it can still be estimated (Pärtel *et al.*, 2011). The choice of method mostly depends on the study scale (de Bello *et al.*, 2016; Lewis *et al.*, 2016a). For small scale studies, experimental and expert opinions can be used. For experimental design, one can sow additional species which are absent from a study site and are preferably collected from neighbouring sites and observe their success. For the expert opinion method, local experts can advise or make an educated guess of the species which are currently absent from study site although potentially suitable. At the larger study scale, only mathematical methods are possible due to difficulties in conducting experiments over large spatial scales and expert opinions covering large extent are scarce. One option is to use species distribution modeling, which has seen wide use in ecology and nature conservation (Elith *et al.*, 2006; Thuiller *et al.*, 2006). With this method, we develop a bioclimatic envelope around one species and try to estimate species suitability to other sites where it is currently absent but potentially suitable based on environmental similarity (Guisan & Thuiller, 2005). Another mathematical method to use is the species co-occurrence index (Beals, 1984), also known as Beal’s index (Ewald, 2002). This method is based on the idea that species that co-occur often need similar environmental and ecological conditions. This co-occurrence index uses given species co-occurrences with other species in order to estimate species suitability to the sites where it is

currently absent but potentially suitable (Ewald, 2002; Ronk *et al.*, 2015; Lewis *et al.*, 2016a). While both mathematical methods serve a similar aim to predict species suitability at other sites, it has not been known how well these methods match in their estimates of dark diversity size and composition.

Dark diversity complements commonly used observed species richness and the most informative aspect might be their relative difference. Using the dark diversity concept, we can calculate the completeness of site diversity (sensu Pärtel *et al.*, 2013 Community Completeness Index). Completeness of site diversity is defined as the log-ratio between observed species richness and dark diversity (Pärtel *et al.*, 2013). This index shows how much of the site specific species pool is actually realized at the site (Pärtel *et al.*, 2013). The completeness of site diversity index has an advantage over observed species richness because it also accounts for the dark diversity of the site. For example, we could have two sites which both have high species richness, but for one site dark diversity is low and high for the other. Then at a relative scale, these sites will have different realization of their site specific species pool. This difference between sites would not have been evident using just species richness alone. Therefore, the completeness index could be more favoured in comparative biodiversity studies or in nature conservation over commonly used observed species richness.

It is better that some species should remain in dark diversity (Pärtel *et al.*, 2016). From a nature conservation perspective, alien species should be preferentially kept in dark diversity, since eradication from the whole region is often unrealistic (Lewis *et al.*, 2016b). Alien species pose a serious threat to ecosystem stability and native biodiversity and in the face of climate change it is a growing concern to nature conservation (Hulme *et al.*, 2009; Butchart *et al.*, 2010; Bellard *et al.*, 2013; Lewis *et al.*, 2016b). Dark diversity can be estimated separately for native and alien species, and we can estimate how much of the respective native and alien species pool is actually realized at the site (Pärtel *et al.*, 2013). A greater number of potential alien species in the region increases the probability that some alien species could have detrimental impacts. Therefore, the dark diversity concept can be used as an early warning for future invasions. Comparing native and alien species completeness could indicate potential future invasion risks to the site. For example, if completeness of native species is high relative compared to completeness of alien species, then most of the native species that could potentially disperse and tolerate local ecological conditions are already present at the site compared to suitable alien species (dark diversity of alien species), which are absent. This shows that potential invaders are already in the region and could potentially invade the study site. Therefore, calculating the difference between native species completeness and alien species completeness could give a hint of potential future invasion risk for sites which could be more prone to invasion. In these sites, if observed species richness is going to increase, it would likely be at the expense of alien species (Ellis *et al.*, 2012).

Exploring the dark diversity of study sites opens a new perspective to understand biodiversity. For example, dark diversity concept can be used to explore how communities are assembled (Riibak *et al.*, 2015), i.e., why we observe species as they are distributed nowadays and why some species remain in dark diversity (Ronk *et al.*, 2015). It is important to understand which natural and anthropogenic factors affect native and alien species (Rejmánek, 2000). This knowledge would potentially help us to understand why some regions are more invaded and which factors would assist future invasion. There is general agreement that climate shapes large scale species distributional ranges (Thuiller *et al.*, 2005a). It has been suggested that species are still in disequilibrium with current climate and are in fact still dispersing in Europe (Svenning & Skov, 2005). This effect has been found especially strong for alien species (Williamson *et al.*, 2009). Although it has been found that high human population coincides with high species richness (Araújo, 2003) and humans are primary dispersal vector alien species, it is not known how different anthropogenic and natural factors influence completeness of site diversity of native and alien species.

The dark diversity concept can be merged with functional ecology. Recently it has been found that at small spatial scales, observed species in European grasslands species have longer maximum dispersal distances compared to species which are in dark diversity, supporting the notion that many species could be dispersal limited (Riibak *et al.*, 2015). Thus, examining dark diversity might inform us about potential limitations of local diversity. Therefore dark diversity (completeness of site diversity) could be a valuable tool also in nature conservation (Lewis *et al.*, 2016b). It can be used to measure the success of the site restoration or to monitor how well the protected areas are functioning. For example, if species are “moving” from observed to dark diversity, this could indicate that local extinctions are occurring at the site. In the other hand, dark diversity can be seen as a buffer for protected areas. If species of interest are still in dark diversity, it means that those species are still in the region and can potentially disperse to protected area (Lewis *et al.*, 2016b). But if dark diversity decreases and species are not “moving” to observed species richness, then changes are occurring in the site specific species pool, meaning that suitable species for protected area are not even present in the region.

Large scale datasets are always to some degree imperfect, especially when the study grain or extent is large (Vellend *et al.*, 2008). These dataset compilations represent a long-term effort by many individuals, which in turn could introduce possible regional sampling bias. The only grid-based data source that covers the whole Europe is Atlas Florae Europaeae (Jalas & Suominen, 1972–1994; Jalas *et al.*, 1996; Jalas *et al.*, 1999; Kurtto *et al.*, 2004). This atlas covers ca. 20% of species in Europe and has some regional under-sampling biases (Nogués-Bravo & Araújo, 2006; Kowarik, 2011; Kalwij *et al.*, 2014). It is therefore essential to verify if those sampling biases are large enough to have some confounding effects on the results. One option would be to compare different large-scale species distribution datasets that have similar spatial grain

and extent to verify if taxonomic representativeness and species richness patterns are similar (Kalwij *et al.*, 2014). Although large scale species distribution data are relatively scarce, especially in Europe, another option would be using some regional datasets to identify regions that could be geographically more poorly represented. How Atlas Florae Europaeae represents the variation of the total plant diversity has not yet been evaluated.

Objectives of the thesis

The purpose of this thesis was to use the dark diversity concept to quantify European plant diversity on relative terms (how much is observed, how much is absent) by determining the variation of site specific species pools using Atlas Florae Europaeae and several regional datasets within Europe. We use different mathematical methods to estimate dark diversity and look if the merging of different dark diversity estimates could give new insights. We explore how dark diversity can be used in nature conservation and invasion ecology and test whether Atlas Florae Europaeae represents a suitable subset of the total plant diversity in Europe.

The main aims of the thesis:

- (1) To estimate how dark diversity and completeness of site diversity is distributed compared to observed species richness. We hypothesized that while observed species richness shows a negative relationship with latitude, the completeness of site diversity shows no significant relationship due to co-variation of the site specific species pools.
- (2) To compare how well two mathematical methods, species co-occurrence and species distributional modeling, match in estimating dark diversity (size and species composition) in Europe. We hypothesized that both methods will carry unique information regarding dark diversity and new insights could be gained by defining dark diversity semi-quantitatively.
- (3) To quantify and map alien species distribution in absolute and relative terms. We explore observed alien species richness, completeness of alien species site diversity and exploring differences between native and alien completeness of site diversity. We hypothesized that completeness of site diversity is higher for native than for alien species at the European scale.
- (4) To explore how different native species and alien diversity metrics are related to different natural and anthropogenic factors. We hypothesized that relative diversity metrics give new information compared to observed species richness.
- (5) To outline how the dark diversity concept can be applied in nature conservation.
- (6) To determine how observed species richness is represented in Atlas Florae Europaeae by comparing it with different continental and regional datasets within Europe. We hypothesized that Atlas Florae Europaeae is a representative subset of total plant richness in Europe.

METHODS

Data

In papers I, II, III and V we used ‘Atlas Florae Europaeae’ (Jalas & Suominen, 1972–1994; Jalas *et al.*, 1996; 1999; Kurtto *et al.*, 2004). This atlas contains presence-absence distribution data for 4123 species or sub-species in Universal Transverse Mercator (UTM) grid cells with a resolution of 50 x 50 km. In papers I, II, and III the study area was delimited in the east along the political boundaries of the Russian Federation, Ukraine, Belarus and Moldova. This restriction was used because Atlas Florae Europaeae offers incomplete data in these regions (Manne & Williams, 2003; Nogués-Bravo & Araújo, 2006). We also excluded the Azores, Canary and Svalbard Islands since most of grids contained ocean. These delineations of the area represent a trade-off between geographical coverage and completeness of data. In paper V we additionally used Atlas of North European Vascular Plants North of the Tropic of Cancer (Hultén & Fries, 1986). This range atlas consists of 1936 range maps and has species distribution data for about 2600 taxa.

In paper I we used regional datasets from Spain (www.anthos.es), Germany (www.floraweb.de/), British Isles (<http://www.brc.ac.uk/plantatlas/>) and Finland (Lampinen & Lahti, 2013, www.luomus.fi/kasviatlas/). In paper II we additionally used regional data from Estonia (<http://efloora.ut.ee/Eesti/index.html>), the Netherlands (<http://soortenbank.nl/>), Switzerland (<http://www.infoflora.ch/de/flora/art-abfragen.html>) and Catalonia (<http://www.floracatalana.net/>). In paper III we also included Iceland (<http://www.floraislands.is/blom.html>). These regional datasets have a spatial resolution of roughly 10 x 10 km except for Germany which had roughly 12 x 11 km grid cells and Netherlands and Switzerland with a spatial resolution of 5 x 5 km. We aggregated 5 x 5 km resolutions to 10 x 10 km to better match the scale of the other regions.

In paper III each species was classified as either native or alien. Atlas Florae Europaeae provides floristic status individually for each grid cell, defining alien species as those introduced after 1500 AD (Pyšek *et al.*, 2002a). For regional analysis, we obtained the floristic status of each species in each region from the Euro+Med database (www.emplantbase.org), which provides a list of alien and native species for vascular plants of Europe and the Mediterranean region. Similarly to Atlas Florae Europaeae this database also defines alien species as those introduced after 1500 AD. Alien status for species was treated at regional level.

In paper III we used several natural and anthropogenic factors which have been shown to influence large-scale species distributions. Natural factors included climatic parameters and landscape heterogeneity. (1) mean annual temperature and (2) mean annual precipitation at spatial resolution of 5' were obtained from WorldClim database (Hijmans *et al.*, 2005). We calculated average precipitation and temperature for 50 x 50 km Universal Transverse Mercator (UTM) and regional 10 x 10 km grid cells. Log-transformed values of

precipitation were used in the statistical analysis. (3) landscape heterogeneity was quantified by effective number of habitat types (Jost, 2006) of Corine 2006 level 2 land-use types (Bossard *et al.*, 2000). Landscape heterogeneity quantifies the diversity of habitat types within a site.

Anthropogenic associated variables characterized human influence. (1) current human population density was obtained from the HYDE 3.1 database (most recent available record 2005 (Goldewijk *et al.*, 2011)). The spatial resolution of the population density was 5'; we averaged data for 50 x 50 km and 10 x 10 km grid cells. Log-transformed values of human population density were used for statistical analysis. (2) the relative amount of agricultural land use was calculated using data from Corine 2006 label 1 land-use types as $\ln(\text{Agricultural areas} / (\text{Forest and semi natural areas} + \text{Wetlands areas}))$.

Determining dark diversity

In papers I, II, III we used three sequential filters in order to determine dark diversity for each site: geographical, biogeographical and environmental filter. Analyses were done separately for the European and each regional dataset. In this thesis we treat a grid cell as one site. In order to apply the geographical filter to account for species potential dispersal we used 500 km radii at the European scale and 300 km radii at the regional scale around each site. To apply the biogeographical filter we used dispersion fields (Graves & Rahbek, 2005) in order to distinguish areas sharing similar biogeographic history and environmental conditions within the geographically delimited areas. We included species from the area which contain at least half the species found in the target site (Carstensen *et al.*, 2013). In order to estimate species environmental suitability for a site, we used a species co-occurrence index. This index quantifies the probability of joint occurrence of a particular species with other species (Beals, 1984; Ewald, 2002; Lewis *et al.*, 2016a):

$$p_{ij} = \frac{1}{S_i} \sum_k \frac{N_{jk} I_{ik}}{N_k}$$

where P_{ij} is the probability that species j occurs in site i . S_i is the number of species at site i (excluding species j), N_{jk} is the number of joint occurrences of species j and k ($j \neq k$), I_{ik} is the incidence (0 or 1) of species k in site i . N_k is the number of occurrences of species k . Each species was assigned a threshold value for inclusion into dark diversity. A species was included into the dark diversity when it was absent from a grid cell and its occurrence-probability was higher than 5% from the values in grid cells where the species was actually present. Statistical tests were performed using R ver. 3.0.2 (R Core Team, 2015) and the 'beals' function within the 'vegan' package (Oksanen *et al.*, 2013) to perform co-occurrence probability calculations.

Dark diversity was used to calculate the completeness of site diversity sensu community completeness index according to Pärtel *et al.* (2013) as:

Completeness of site diversity: $\ln(\text{Observed richness}/\text{Dark diversity})$.

We mapped and compared observed species richness (actual species count in the grid cell) distribution with dark diversity and completeness of site diversity. In paper II we also estimated dark diversity by the species distribution modeling method (SDM) and compared it with species co-occurrence method (SCO). We used generalized additive models (GAM). Generalized additive models were fitted using logit as the link function and a binomial error distribution. We used data-splitting (80% of the data was used for calibration and 20% for evaluation), which we ran on different random selections. The resultant species occurrence probabilities were transformed into species presences and absences using a threshold giving the best quality of predictions, evaluated as the best score of true skill statistic (TSS, Allouche *et al.*, 2006). We used “BIOMOD2” (Thuiller *et al.*, 2009) package (R package version 3.1-25) for species distribution modeling.

To compare how well the two mathematical methods, species co-occurrence and species distributional modeling, match in estimating dark diversity we compared dark diversity sizes (number of species in dark diversity) by using these as variables in Type II regression. We also compared species composition in dark diversity by overlap coefficient (Kowalski, 2011). This index is defined as the number of species common to both methods divided by the smaller dark diversity size of the two methods. To obtain semi-quantitative values of dark diversity, we counted species which were assigned to dark diversity by both methods (consensus dark diversity), or by one method (composite dark diversity).

In paper III we used several absolute and relative metrics for alien and native species to explore how these diversity metrics are related to different natural and anthropogenic factors in Europe. Native species and alien richness were calculated as the count of actual species in the grid cell. Native completeness (completeness of site diversity for native species) was calculated as the log-ratio of native species richness divided by dark native diversity. Alien completeness (completeness of site diversity for alien species) was calculated as the log-ratio of alien species richness divided by dark alien diversity. The completeness difference was calculated as completeness of native species site diversity minus completeness of alien species site diversity.

Statistical and sensitivity analyses

In paper I we regressed observed species richness and completeness of site diversity against latitude to explore the latitudinal gradient relationship. In paper III we examined whether alien completeness is less than native completeness by paired t-test. The effects of the explanatory variables on the diversity metrics was assessed with linear mixed effect models with the ‘lme’ function in the R package ‘nlme’ (Pinheiro *et al.*, 2015). We standardized all the explanatory natural and anthropogenic variables to have a mean of zero and a standard deviation of one. In regional analyses we used region as a random factor in the models. We measured the effect of spatial autocorrelation in our models with Moran’s *I* on normalized residuals of the simple models. Due to strong spatial autocorrelation, we fitted linear mixed effect models with exponential spatial correlation structure and a nugget value allowed (Dormann *et al.*, 2007). We used azimuthal equal-area metric x and y coordinates.

In paper I we tested whether Atlas Florae Europaeae represents the total observed richness by using independent datasets from Spain, Germany, British Isles and Finland. We related the number of species common to both datasets to those not contained in the Atlas Florae Europaeae. Species richness values were ln-transformed. We calculated R^2 and the slope of the major axis type II regression. The ‘lmodel2’ function within package ‘lmodel2’ (Legendre, 2014) was used to perform major axis (type II) regression calculations.

In paper V we first determined species that occurred both in Atlas Florae Europaeae and Atlas of North European Vascular Plants North of the Tropic of Cancer. We calculated the Jaccard index for each site (grid cell) to determine how the similarity between the two atlases was distributed. The Jaccard index shows the difference in species list similarity and is calculated by dividing the intersection of species by the union of species.

RESULTS

Observed species richness distribution comparison with dark diversity and completeness of site diversity

Observed species richness showed a latitudinal gradient, being low in northern and higher in southern Europe (Fig. 1A). However, observed species richness values were somehow lower in some regions within the Mediterranean area. Also dark diversity generally mimics the latitudinal gradient but values are generally smaller compared to observed species richness (Fig. 1B). Compared to the observed species richness pattern, completeness of site diversity exhibited no latitudinal gradient. The two slopes from standardized values differ significantly ($t = -12.8$, $df = 3134$, $p < 0.001$). We can find sites with high completeness at both high latitudes and low latitudes (Fig. 3C)

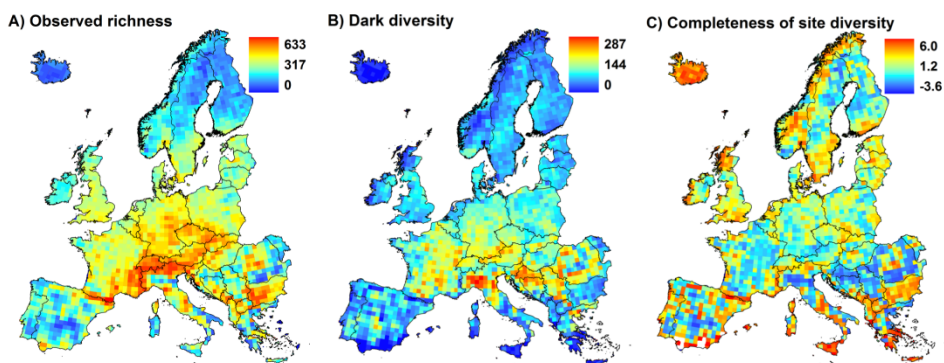


Figure 1. Plant diversity at the European scale: A) Observed species richness – based on actual recordings from 50 x 50 km grid cells, B) Dark diversity – the number of absent species from the site specific species pools and C) Completeness of site diversity – $\ln(\text{observed richness}/\text{dark diversity})$. Figures are from Ronk *et al.*, (2015).

Dark diversity estimates by species distribution modelling and species co-occurrence methods

Both mathematical methods showed similar dark diversity sizes at the European scale (Fig.2). Dark diversity estimates exhibit strong positive correlation but Type II regression slopes differed from the 1:1 line, showing that both methods also carry unique information. Both methods were roughly most similar at intermediate dark diversity values. Species composition overlap of the two methods was about 75% (the first and the third quartiles are 63% and 78%).

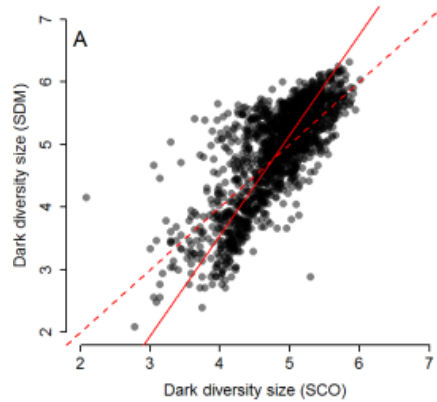


Figure 2. Relationship between dark diversity (ln transformed) by species co-occurrence (SCO) and species distribution modeling (SDM) methods ($R^2 = 0.61$, slope = 1.6, 95% CI 1.5 and 1.7, $p < 0.001$) at European scale. Solid line represents Type II regression line and dashed line 1:1 relationship. Regression lines deviate from 1:1 lines. Figures are from Ronk et al. (2016).

Consensus (species estimated by both methods) and composite (species estimated by at least one method) dark diversity showed similar patterns throughout Europe (Fig. 3A, 3B). Generally dark diversity was low in northern and high in southern Europe, although there were some regional differences between the two methods. Compared to consensus dark diversity, composite dark diversity showed higher dark diversity sizes especially in central Europe and the Iberian Peninsula (Fig. 3B).

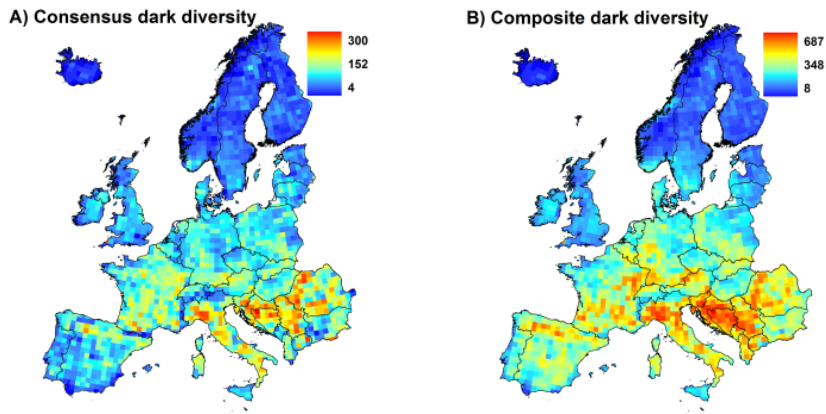


Figure 3. Consensus and composite dark diversity estimates (species predicted by both or one method) at the European scale A) Consensus dark diversity and B) Composite dark diversity. Figures are from Ronk et al. (2016).

Alien species diversity metrics

Observed alien species richness is greatest in NW Europe and lower in the Mediterranean region at the European scale. In contrast to observed alien richness, alien completeness exhibits a scattered pattern across Europe. Sites with high completeness are located in both northern Europe and southern Europe. Central Europe contains mainly moderately complete sites (e.g. in Germany), although sites in France show rather low completeness. Completeness difference (completeness of native species minus completeness of alien species) is largely positive ($t = 37.1$ $df = 1406$, $p < 0.001$). This indicates that relatively few alien species potentially able to disperse and establish in a given site are present compared to how much of the native species pool is realized. Completeness of alien species site diversity was rather lower compared to native species site diversity in northern Europe, thus indicating potential future invasion risks in that region. Especially high values of completeness difference were found in the Baltic States, Scandinavia and Iceland (Fig. 4).

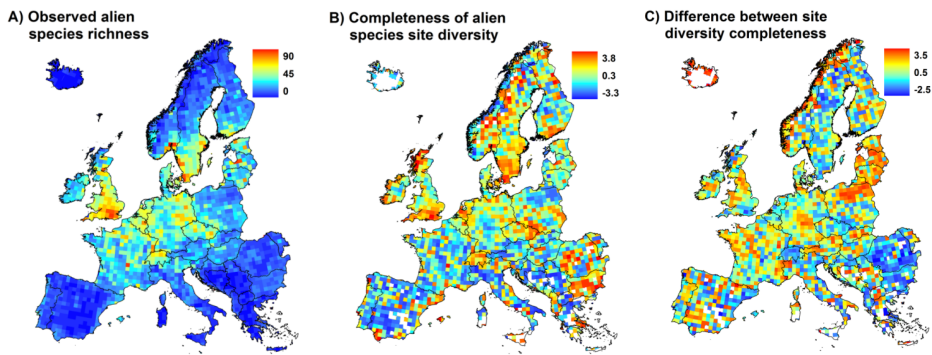


Figure 4. Alien species diversity metrics: A) Observed alien species richness, B) Completeness of alien species site diversity (how much of the alien species pool is realized), C) Completeness difference between native species site diversity and alien species site diversity. Figures are from paper III.

Native and alien species association with natural and anthropogenic factors

At the European scale native species richness shows a positive association with human population density and land-use heterogeneity in both datasets (Table 1). At the European scale natural factors also play a role; precipitation show positive effect and temperature show negative effect on native species richness. Agricultural land-use also shows a negative effect on native species richness at the European scale. Alien species richness showed a positive relationship only

with human population density, but on regional scale also temperature, agricultural land-use and land-use heterogeneity plays a role (Table 1).

Native completeness is related positively with land-use heterogeneity and negatively with agricultural land-use in both datasets, (Table 1). Additionally, native completeness at the European scale is negatively associated with temperature and positively with human population density. Opposed to alien species richness, alien completeness is negatively associated with agricultural land-use. Similarly to alien species richness positively with human population density at both the European and regional scales. Alien completeness at the European scale shows significant relationships mainly with anthropogenic factors.

Completeness difference is associated negatively with human population density at both scales (Table 1). At the European scale, completeness difference exhibits a positive association with agricultural land-use. At the regional scale temperature and land use heterogeneity also show positive relationships. In short, alien species completeness and completeness difference are associated with anthropogenic rather than natural factors at European scale.

Table 1. Summary results of the spatially-informed linear mixed effect model relating observed native and alien species richness and respective completeness and completeness difference to natural and anthropogenic factors. Positive relationship (+), negative relationship (-), non-significant relationship (NS). Significance indicated by the number of symbols: $p < 0.05$ (+ ; -), $p < 0.01$ (++; --), $p < 0.001$ (+++; ---). A single indication is shown in a cell when the result applied to both Europe and regions. Table is from paper III.

		Native richness	Alien richness	Native completeness	Alien completeness	Completeness difference
Temperature	Europe	---	NS	---	NS	NS
	Regions	NS	+++	NS	---	+++
Precipitation	Europe	++	NS	NS	NS	+
	Regions	NS		++	+	NS
Land-use heterogeneity	Europe	+++	NS	+++	+	NS
	Regions		+++		NS	+
Human population density	Europe		+++	+++		
	Regions	+++		NS	+++	---
Agricultural land-use	Europe	---	NS	--		+
	Regions	NS	+++	---	--	NS

How well Atlas Florae Europaeae represents total species richness

The number of species in Atlas Florae Europaeae is significantly and positively related to the number of species not included in the Atlas Florae Europaeae in the studied regions (Fig. 5). AFE described ca. 95% of the variation of the total biodiversity. In other words, general diversity variation in regional databases is well represented by the variation of the portion of species included in Atlas Florae Europaeae. Also, on the European scale, species richness derived from AFE compared those derived from the Atlas of north European vascular plants generally agree, but some political boundaries emerge, especially in the eastern part of Europe (e.g. Russia, Moldova, Ukraine), making data from those regions potentially unreliable. The Jaccard index show a high level of agreement in species lists between the intersection (species occurring both atlases) of the two atlases (Fig. 5B in V).

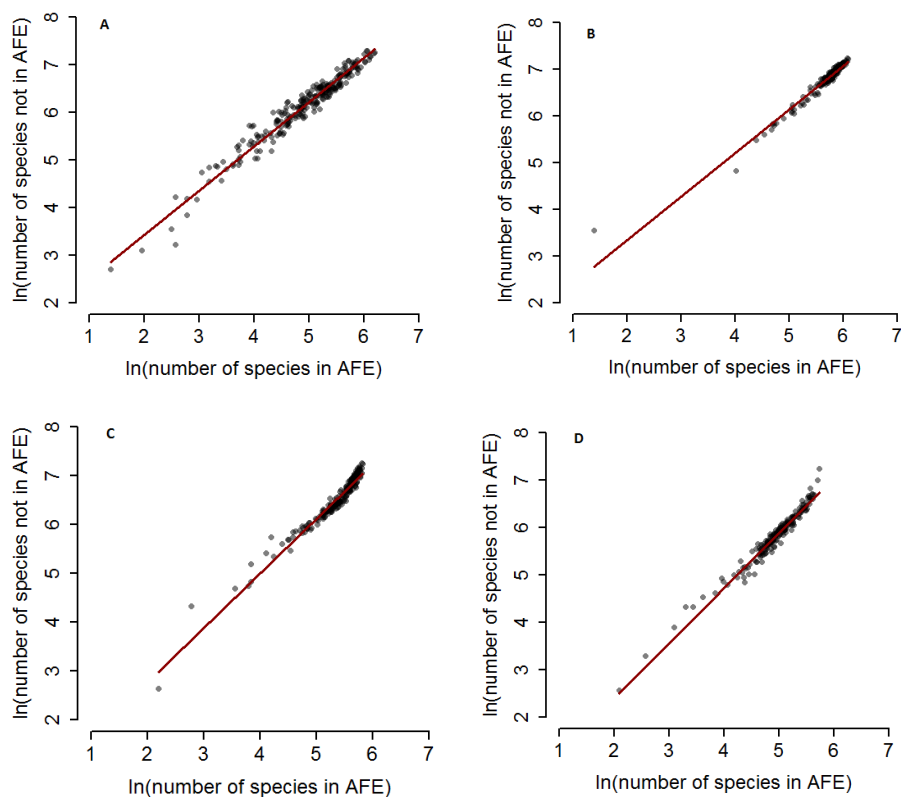


Figure 5. The relationship between the number of species in Atlas Florae Europaeae (AFE) and the number of species not in AFE but present in the following datasets: A) Spain B) Germany, C) British Isles, D) Finland. Major axis (type II) regression lines are shown. Figures are from Ronk *et al.*, (2015).

DISCUSSION

Comparing absolute values of observed species richness across large spatial extents can be insufficient due to the concurrent variation in dark diversity, i.e., the absent part of the site specific species pool (Pärtel *et al.*, 2011; Zobel, 2016). Indeed, we were able to attain new insights in plant diversity patterns at the European scale when observed species richness was expressed at a relative scale accounting for both observed and absent parts within site specific species pools (I, II, III). We found that this new information can have applications in studies on biodiversity and nature conservation when dark diversity (ecologically suitable absent species for a study site) is accounted for (IV). We found that although observed species richness followed a global latitudinal gradient, completeness of site diversity showed a scattered pattern across Europe (I). Both used mathematical methods showed a similar distribution pattern of dark diversity although both methods also carried unique information (II). Quantifying dark diversity semi-quantitatively enabled us to quantify dark diversity more narrowly and more broadly, each of which can serve different purposes depending on the research question (II). For example, dark diversity can be a useful tool in nature conservation, especially in invasion ecology (IV). With dark diversity we can estimate the completeness of alien species. Completeness of alien species in association with completeness of native species revealed areas where risk of future invasion could be higher (III). The accuracy of estimating dark diversity by mathematical methods relies on the completeness of local plant inventories throughout the study system. Our results, however, were robust when sensitivity analyses were applied or independent regional datasets were used (V). Therefore, linking observed and dark diversity can be achievable despite methodological challenges and new insights into species distribution patterns can be obtained.

Dark diversity complements observed species richness

Dark diversity showed a similar distribution pattern as observed richness pattern, being lower in northern and higher in southern Europe (I). Opposed to observed species richness, completeness of site diversity showed a scattered pattern across Europe. Moreover, while observed species richness was related negatively with latitude, the completeness of site diversity showed no relationship with latitude (I). This shows that the realization of the site specific species pool could be high both in northern and southern Europe. Central Europe showed moderately complete sites, which could be due to human influence due to intensive land-use, which has caused local extinctions (Cepelova & Münzbergova, 2012; Ellis *et al.*, 2012, I). Mountainous areas, such as Scandinavia, the Alps and the Pyrenees, tend to exhibit high completeness. Due to topographic variation, evidently more species can find suitable habitats; therefore mountainous areas can also accommodate a large share of site specific species

pools. Also, anthropogenic habitat loss has been smaller in mountainous areas (Sandel & Svenning, 2013). Completeness of site diversity revealed new patterns which were not evident from observed richness. Our results showed that on the European scale the strongest predictors for native species richness were land-use heterogeneity and human population density (III). Similarly, for native species completeness of site diversity, we found that land-use heterogeneity and human population were the strongest predictors. On the regional scale agricultural land-use was a more important predictor than human population density, which turned to non-significant for completeness of site diversity (III). Irrespective of the study scale, we found that anthropogenic factors appeared to be stronger factors than natural.

Dark diversity methods comparison

Testing how two mathematical methods, species co-occurrence and species distribution modeling, estimate dark diversity sizes, we found that dark diversity sizes were similar across Europe (II). Also, estimates of dark diversity sizes exhibited a strong positive correlation although deviating from the 1:1 line, showing that each method carried unique information. This was also evident when we calculated the overlap coefficient for species composition in dark diversity, which was 75% for the two methods (II). This difference in estimations could arise from species frequency. Species co-occurrence method uses only species presences and absences and needs “enough” species co-occurrences with other species (Botta-Dukat, 2012) to include a species in dark diversity (I). Therefore, rare species in the dataset could be disregarded from dark diversity. In contrast, the species distribution modeling method has been found to perform rather poorly for common species with wide environmental niche (Elith *et al.*, 2006).

A combination of different methods in the biodiversity studies has shown great promise (Araújo & New, 2007). Combinations of different methods enabled us to define dark diversity semi-quantitatively by including species from both or one method: consensus and composite dark diversity. Both estimates showed similar spatial patterns, although the distribution of composite dark diversity was smoother (II). Composite dark diversity was also larger than consensus, since we assembled information from the two methods; nevertheless, the distribution pattern was similar. We suggest that consensus dark diversity could be preferred in nature conservation to decide if a particular species should be included in the dark diversity of a site, e.g. for restoration. By contrast, we suggest that composite dark diversity could be used for analyses of large-scale diversity patterns as it contains more information from different methods.

Observed and dark diversity of alien species

Observed alien species richness was highest in NW Europe and lowest in the Mediterranean area (III). In our dataset only recent invaders, also known as neophytes (Pyšek *et al.*, 2002a), were considered alien species. It has been found that invasions in central and northern Europe are typically more recent (Chytrý *et al.*, 2009) compared to the Mediterranean area where some alien species were introduced so long time ago that these are considered native species nowadays (di Castri, 1989). Our analyses showed that land-use heterogeneity, agricultural land-use and human population density were also stronger predictors for alien species richness than climate related factors, similarly as we found for native species richness (III). This suggests that the same factors that influence positively native species can also affect positively alien species (Stohlgren *et al.*, 1999; Davies *et al.*, 2005).

Compared to alien species richness, completeness of alien species showed scattered patterns across Europe (III). At the European scale, alien species richness showed a positive relationship only with human population density. Completeness of alien species site diversity is also related positively to human population density. Completeness of alien species additionally revealed that agricultural land-use was negatively associated with completeness of aliens (III). Indeed, it has been found that only ancient invaders are associated with agriculture, whereas more numerous recent invaders have other target habitats (Pyšek *et al.*, 2005). Also, humans can affect biodiversity by creating habitat types more suitable for alien species, or act as a dispersal vector (Kowarik, 2011).

We found that completeness difference between native and alien species site diversities had high values in the northern part of Europe, especially in Baltic States and in Scandinavia (III). Consequently, there could be higher future invasion risk in these regions, because relatively many potential alien species are present in the surrounding regions (III). Lambdon *et al.* (2008) found that most European alien plant species arrived in Europe at the beginning of the 20th century. Consequently, most alien species have not yet filled their climatically possible ranges and continue to disperse more actively than native species (Williamson *et al.*, 2009; Lososová *et al.*, 2012). This was further supported in our dataset because we found that completeness of alien species was mostly less than completeness of native species site diversity (III). We also found that southern Europe exhibits lower completeness of native species. Nonetheless, low values do not grant a lower risk of future invasion, since our method does not account for source regions outside Europe (Thuiller *et al.*, 2005b; Bellard *et al.*, 2013). There are several similar Mediterranean-type areas in the world that could act as donors of alien species to Europe (Feng *et al.*, 2011; Kalusová *et al.*, 2014).

We found that completeness difference was less in densely populated regions (III). Urban areas tend to support more alien species than native species due to high levels of human activity (Wania *et al.*, 2006; Lososová *et al.*, 2012).

By contrast, completeness difference was greater at sites with high landscape heterogeneity at the European scale (III). This suggests that alien species might have less ability to invade in different habitat types than native species (Lambdon *et al.*, 2008). The completeness difference also showed a positive relationship with temperature at the regional scale, and with precipitation at the European scale. This agrees with the observation that warm and wet tropical regions have fewer invasions than temperate regions, attributed to quicker post-disturbance recovery in wet and warm ecosystems leaving fewer disturbed sites for alien species to colonize (Rejmánek, 1996).

Dark diversity and nature conservation

The dark diversity concept can be an additional tool in nature conservation and can supplement existing approaches (Lewis *et al.*, 2016b). For example, extant irreplaceability (species endemism, Myers *et al.*, 2000; Brooks *et al.*, 2006) and vulnerability (risk of biodiversity loss) (Wilson *et al.*, 2005) indices in nature conservation do not provide information on a site or region's current biodiversity relative to its potential biodiversity, while the completeness of site diversity index looks at how much of the site specific species pool is actually realized at the site (Pärtel *et al.*, 2013). Therefore, rather complete sites should imply greater stability of the site, which can potentially act as a refuge for species. In addition, completeness of site diversity can also be used to compare sites irrespective of the trophic levels, such as insects, birds and plants, making different groups of organisms more comparable with each other (Pärtel *et al.*, 2013). Therefore, completeness with respect to the site specific species pool can be beneficial for addressing conservation decisions (IV).

Often ecological restoration requires a reference state to be defined, typically the pre-disturbance state. Therefore, it is essential to understand which species from the species pool are to be recouped (Sundermann *et al.*, 2011). Comparing the site specific species pool of the reference site with the degraded site can provide additional information concerning the likelihood of achieving successful restoration. If large differences exist between the two species pools (degraded and reference site), restoration success of the site to the pre-disturbance state is unlikely to be effective. However, if a suitable species exists in the wider region and has a probability to disperse to and establish in the site, the chances of successful restoration could be greater (IV). Therefore, conserving dark diversity is vital from a restoration point of view.

How well Atlas Florae Europaeae represents total species richness

The use of Atlas Florae Europaeae has been questioned because northern and central regions are better represented than southern regions (Araújo, 2003; Keil *et al.*, 2012; Kalwij *et al.*, 2014). At lower latitudes we can find a decline in observed species richness, which might be due to a lower sampling effort. While we potentially underestimate the observed species richness at low latitudes, we also underestimate dark diversity (fewer co-occurrences between species), therefore completeness of site diversity is not affected much, showing that the results are robust (I). We found that Atlas Flora Europaeae shows little difference in variation of species richness from regional databases derived from sampling at a scale least 25 times smaller (I). The species richness of taxa included in the atlas described ca 95% of variation of the total biodiversity. This confirms that the Atlas Florae Europaeae is comparable to regional large-scale plant occurrence data-sets. Moreover, richness patterns derived from this atlas compared with those derived from the Atlas of north European vascular plants generally agree (V). Overall our results confirm that AFE is a representative subset of the total plant diversity across Europe.

CONCLUSIONS

Accounting for absent but suitable species in biodiversity studies can improve our understanding of processes why we observe species as they are distributed nowadays and why some species remain in dark diversity. Especially completeness of site diversity can be a valuable metric in nature conservation and biodiversity studies, because it makes different study sites or regions more comparable with each other. Completeness of site diversity index accounts for both observed and dark diversity. (1) While observed species richness showed a negative relationship with latitude, completeness of site diversity showed a non-significant relationship with latitude. (2) While the methodological toolbox for dark diversity is still developing, we found that combining two mathematical methods might be promising. Although the two methods resulted in similar dark diversity sizes across Europe, they also carried some unique information about dark diversity. (3) We found that completeness of native species site diversity was larger than alien species completeness, showing that alien species are still in fact dispersing in Europe. We found that future invasion risk could be higher in the northern part of Europe. (4) On European scale alien species richness showed a positive relationship only with human population density. Completeness of alien species site diversity revealed that agricultural land-use had a negative effect on completeness of alien species. (5) From a nature conservation point of view, we suggest that dark diversity can be a valuable tool both for area restoration as well as for monitoring. (6) We found that that biodiversity at a relative scale can be less sensitive to inaccuracies in large-scale datasets and Atlas Florae Europaeae is a representative subset of total plant richness in Europe. Overall, although dark diversity cannot be sampled directly, it can be still estimated and it can be beneficial for addressing both theoretical and applied biodiversity questions.

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SUMMARY IN ESTONIAN

Taimede mitmekesisus Euroopas: vaadeldud ja tume elurikkus

Elurikkuse hoidmine on looduskaitse olulisemaid eesmärgi. Traditsiooniliselt on kasutatud elurikkuse mõõdikuna mingil maa alal esinevate liikide arvu ehk liigirikkust. Selle abil on määratud elurikkuse tulipunkte, testitud ökoloogilisi reegleid (nt. liigirikkuse muutumine piki laiuskraadi) või piiritletud looduskaitsealasid. Vähem on tähelepanu pööratud ohule, et liigirikkus elurikkuse mõõdikuna võib mõnel juhul olla ka ebapiisav. Vaadeldes vaid liikide arvu, ei arvestata liigifondide varieerumist. Liigifondiks nimetatakse liikide kogumit, mis kas juba kuuluvad kooslusesse (vaadeldud liigirikkus), või võiksid sinna potentsiaalselt levida ja sealsetes ökoloogilistes tingimustes elada (tume elurikkus). Täieliku elurikkuse pildi saamiseks tuleks lisaks vaadeldud liigirikkusele arvestada ka puuduolevate, kuid ökoloogiliselt sobivate liikidega ehk tumeda elurikkusega.

Kuigi tumedat elurikkust ei saa mõõta nagu vaadeldud liike on seda siiski võimalik hinnata. Et hinnata tumedat elurikkust on vaja teada liikide levikut piirkonnas ja liikide keskkonnameelistusi. Selleks, et lugeda puuduolevat liiki tumeda elurikkuse osaks peab liik läbima erinevaid filtreid: 1) geograafiline filter: liik peab olema võimeline levima uurimisalale ja 2) keskkonnafilter: liik peab olema võimeline taluma alal valitsevaid keskkonnatingimusi. Tumeda elurikkuse leidmiseks sobiva meetodi valik sõltub peamiselt töö skaalast. Kui väiksemaskaalaliste tööde puhul on võimalik tumeda elurikkust leida eksperimenti või ekspertarvamuse abil, siis suureskaalaliste tööde puhul on võimalik tumedat elurikkust hinnata vaid matemaatiliste meetoditega.

Tume elurikkus täiendab vaadeldud liigirikkust. Kasutades tumeda elurikkuse käsitlust on võimalik leida ala täielikkuse indeks. Ala täielikkus näitab, kui suur osa potentsiaalsest liigifondist on tegelikult uurimisalal realiseerunud. Võrreldes vaadeldud liigirikkusega võtab täielikkuse indeks arvesse korraga nii vaadeldud kui ka tumeda elurikkuse. Seetõttu võiks antud indeks olla eelistatum elurikkuse mustrite uurimisel ja looduskaitsetes kui tavaliselt kasutatud vaadeldud liigirikkus.

Kasutades tumedat elurikkust on võimalik saada aimu, mis elurikkust piirab ehk miks osad liigid jäävad uuritud aladel tumedasse elurikkusesse. Seetõttu on tumeda elurikkuse kontseptsioon eriti väärtuslik looduskaitsetes. Kui liigid „liiguvad“ vaadeldud liigirikkusest tumedasse elurikkusesse, siis võib see vihjata probleemidele uuritaval aladel – toimuvad kohalikud väljasuremised. Samas ei ole olukord veel lootusetu, kui looduskaitsele huvipakkuvad liigid on olemas tumedas elurikkuses, on liigid regioonis veel olemas ja võivad asjaolude paranedes uurimisale tagasi levida. Tumedat elurikkust saab kasutada kui ka varajast hoiatust võimalike võõrliikide invasioonide eest. Kui võõrliigid on juba tumedas elurikkuses, siis see tähendab, et nad on olemas juba ümbritsevas regioonis ja on potentsiaalselt võimelised ka levima uurimisalale.

Käesoleva töö eesmärk oli kasutada tumeda elurikkuse kontseptsiooni, et hinnata taimede elurikkuse jaotust Euroopas. Me kasutasime Euroopa taimede levikuatlast „Atlas Florae Europaeae” ja mitmeid regionaalseid andmestike. Tumeda elurikkuse leidmiseks rakendasime erinevaid matemaatilisi meetodeid ja uurisime erinevate meetodite ühiskasutamise perspektiive. Me pakkusime välja tumeda elurikkuse rakendusi looduskaitstes ja invasiooniökoloogias. Samuti hindasime, kui hästi pooleliolev „Atlas Florae Europaeae” sobib esindama kogu Euroopa taimede liigirikkusest.

Töö peamised eesmärgid olid:

1. hinnata kuidas tume elurikkus ja ala täielikkus on võrreldes vaadeldud liigirikkusega Euroopas jaotunud.
2. võrrelda, kuidas kaks matemaatilist meetodit – liikide koosesinemine ja liikide leviku modelleerimine – hindavad tumeda elurikkuse suurust ja koosseisu.
3. hinnata ja kaardistada võõrliikide levik absoluutses ja suhtelises skaalas. Leida võõrliikide liigirikkus ning täielikkus, ja võrrelda seda looduslike liikide vastavate näitajatega (nt. looduslike ja võõrliikide täielikkuse vahe).
4. hinnata kuidas erinevad looduslike ja võõrliikide elurikkuse indeksid on seotud peamiste keskkonna- ja inimõjuliste teguritega.
5. välja tuua tumeda elurikkuse kontseptsiooni peamised rakendused looduskaitstes.
6. teha kindlaks kui hästi „Atlas Florae Europaeae” esindab kogu taimede elurikkuse jaotumist.

Käesolevas töös saime kinnitust, et tumeda elurikkuse kaasamine vaadeldud elurikkusele andis olulist uut informatsiooni taimede mitmekesisuse levikumustrite kohta üle Euroopa. Kui tumeda elurikkuse levikumuster oli üldjoontes sarnane vaadeldud liigirikkusele, siis suured ning väikesed täielikkuse väärtused oli hajali üle kogu Euroopa.

Analüüsides selgus, et vaadeldud liigirikkus järgis üldtuntud negatiivset suhet laiuskraadiga. Sarnaselt käitus ka tume elurikkus. Ala täielikkus samas ei näidanud statistiliselt olulist seost laiuskraadiga. See tähendab, et suure täielikkusega alasid võib leida nii Põhja- kui Lõuna-Euroopas. Kesk-Euroopa näitas pigem mõõdukat täielikkust, mis võib olla põhjustatud inimtekkelistest kohalikest väljasuremistest. Töös kasutatud mudelid näitasid, et looduslikku liigirikkust mõjutasid positiivselt kõige enam maastiku mitmekesisus ja inimtihedus. Samad tegurid mõjutasid enam ka looduslike liikide täielikkust. Me leidsime, et inimesega seotud tegurid mõjutasid nii loodusliku liigirikkust kui ka täielikkust enam kui keskkonnafaktorid.

Mõlemad kasutatud matemaatilised meetodid – liikide koosesinemine ja liikide leviku modelleerimine – andsid üldjoontes sarnaseid tumeda elurikkuse suurusi, kuid mõlemad meetodid andsid ka unikaalset informatsiooni. Seetõttu võib olla kasulik meetodeid kombineerida ja leida tume elurikkus nii kitsalt kui ka laialt. Kitsa tumeda elurikkuse korral võtame tumedasse elurikkusesse liigid, mis olid ennustatud mõlema meetodi poolt ja laia puhul lisame liigid, mida vaid üks meetoditest määras tumedasse elurikkusesse. Kitsas tume elurikkus võiks

rakendust leida looduskaitstes ja üksikute liikide uurimisel, kuna need liigid on prognoositud mõlema meetodi poolt ja prognoosi usaldusväärsus on suurem. Lai tume elurikkus võiks olla kasulik elurikkuse mustrite uuringus, kuna sisaldab enam informatsiooni võimaliku tumeda elurikkuse kohta. Üldjoontes oli nii kitsa kui laia tumeda elurikkusse üleeuroopaline levikumuster sarnane.

Euroopa võõrliikide liigirikkus näitas ainult positiivset seost inimtihedusega. Sarnaselt liigirikkusega näitas ka võõrliikide täielikkus positiivset seost inimtihedusega, aga lisaks ilmnes negatiivne seos põllumajandusliku maakasutusega. On leitud varemgi, et ainult arheofüüdid (võõrliigid, mis on saabunud Euroopasse enne 1500) on seotud enam põllumajandusega, meie töös kasutusel olnud neofüüdid (hilisemad saabujad) on seotud pigem muude elupaikadega. Looduslike liikide täielikkus oli keskmiselt alati suurem kui võõrliikide vastav näitaja. Võõrliigid on alles aktiivselt levimas kui looduslikud liigid on suuresti (kuigi mitte täiesti) oma võimaliku levila asustanud. Täielikkuste vahe (looduslike liikide täielikkus – võõrliikide täielikkus) oli suurim Põhja-Euroopas, eriti Baltimaades ja Skandinaavias. Järelikult võib just nendel aladel oodata suuremat invasiooniriski võrreldes ülejäänud Euroopaga kuna paljud potentsiaalsed võõrliigid on juba regioonis olemas aga ei ole veel asustanud kõiki võimalikke elupaiku.

Tumeda elurikkuse kontseptsioon on vajalik vahend looduskaitstes täiendades juba olemasolevaid lähenemisi. Täielikkuse indeks näitab kui palju on liigifondist realiseerunud. Seetõttu võiks suure täielikkusega alad olla stabiilsemad ja töötada ohustatud liikide refuugiumitena. Veel enam, täielikkust saab leida erinevatele organismide rühmadele. Täielikkuse indeks töötab „ühtse valuutana“ ja seetõttu on võimalik võrrelda omavahel näiteks taimede, lindude ja putukate täielikkust. Nii saavad täielikkuse indeksid erinevatest organismirühmadest olla sisendiks looduskaitseliste otsuste tegemisel. Tume elurikkus on tähtis ka ala taastamise seisukohast. Kui õnnestub leida taastatavale alale kvaliteetne võrdlusala, mis sarnaneb taastatavale alale enne häiringut, siis võrreldes kahe ala liigifonde saab hinnata taastamise võimalikust. Näiteks kui kahe liigifondi vahel on suur erinevus võib arvata, et kahjustatud ala taastamine on väheedukas, kuna puuduvad sobivad liigid liigifondist. Samas kui sobivad liigid on ümbruskonnas olemas, siis ala taastamise võimalus palju suurem. Seetõttu on ka tumedal elurikkusel ala taastamise seisukohast suur tähendus.

Kirjanduses on väidetud, et pooleliolev „Atlas Florae Europaeae“ ei pruugi hästi kajastada tegelikult liigirikkuse varieeruvust, eriti Lõuna-Euroopas kus on palju taimesugukondi, mida ei ole veel kaardistatud. Meie analüüs näitas, et tegelikult on see andmestik esinduslik valim kogu liigirikkusest üle kogu Euroopa. Võrreldes sõltumatute regionaalsete andmestikega, näitas „Atlas Florae Europaeae“ vaid väikest erinevust liigirikkuse mustrites. Lisaks sellele, kui andmestik alahindab vaadeldud elurikkust, siis selle kasutamine alahindab ka tumedat elurikkust ja suhtelises skaalas (täielikkuse indeks) ei ole tulemused kuigi palju mõjutatud.

Kui võtame elurikkuse uuringutes arvesse ka vaatlusalale sobivaid, kuid hetkel puuduolevaid liike, saame paremini aru protsessidest, mis mõjutavad

liikide levikut ja sagedust. Saame leida põhjuseid, miks osad liigid on uurimisalal kohal, aga teised jäävad tumedasse elurikkusesse. Erinevalt vaadeldud liikidest ei saa tumedat elurikkust mõõta otseselt ala ennast uurides. Siiski on seda võimalik hinnata kasutades suureskaalalisi taustaandmeid. Tumeda elurikkuse kontseptsioon on kasulik nii ökoloogia teoorias kui ka looduskaitstes. Looduskaitsele võib olla eriti informatiivne täielikkuse indeks, kuna see hõlmab üheaegselt nii ala vaadeldud liigirikkuse kui ka tumeda elurikkuse.

ACKNOWLEDGEMENTS

A deep bow and my deepest gratitude goes to my supervisor, Meelis Pärtel, for guidance, patience and endless help. I also want to specifically thank Robert Szava-Kovats, who has supported and helped me throughout my studies and has been available even at the darkest times. I had the pleasure of being part of the Macroecology workgroup – our seminars and beer/tea meetings have been inspiring and often relaxing. I would like to thank all our former and present lab members especially Antonio, Jodi, Riin, Jon, Rob, Krista, Aveliina, Pille, Liina, Kersti, Liis, Marge and Madli for a friendly work atmosphere.

I thank Jan Lepš and Francesco de Bello at the University of South Bohemia in the Czech Republic for accommodating me for three months and letting me learn from them.

I also want to thank my family and friends for always supporting me.

This research was supported by the Estonian Ministry of Education and Research, institutional research funding IUT 20-28,20-29, by the European Union through the European Regional Development Fund (Centre of Excellence FIBIR, Centre of Excellence EcolChange) and by Czech Science Foundation (grant P505/12/1296 and grant GB14-36079G, Centre of Excellence PLADIAS).

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Conferences/seminars:

- Oral presentation at the International Association for Vegetation Science conference in Brno, Czech Republic (19.07.15–24.07.15), “Observed and dark diversity of alien and native plant species in Europe: association with natural and anthropogenic factors”.

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- Poster presentation at the International Association for Vegetation Science conference in Tartu, Estonia (26.06.13–30.06.13), “Regional species richness, species pool and community completeness of European plants: association with natural and anthropogenic factors”.
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- Osalemine rahvusvahelisel konverentsil IAVS (International Association for Vegetation Science) Austraalias (01.09.14–05.09.14) suulise ettekandega “Applying the dark diversity concept for plants at the European scale”

- Osalemine rahvusvahelisel konverentsil IAVS (International Association for Vegetation Science) Eestis (26.06.13–30.06.13) poster ettekandega “Regional species richness, species pool and community completeness of European plants: association with natural and anthropogenic factors”
- Osalemine rahvusvahelisel doktorantide konverentsil Tallinnas (16.05.13–17.05.13) “Down to Earth” suulise ettekandega teemal “Regional species richness, species pool and community completeness of European plants: association with natural and anthropogenic factors”
- Osalemine rahvusvahelisel konverentsil GfÖ (Saksamaa, Austria ja Šveitsi ökoloogiaühing) Saksamaal (10.09.12–14.09.12) suulise ettekandega “Alien plant species in Europe: distribution of absolute and relative richness”

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- 2012 Osalemine kursusel (03.09.12–7.09.12) “Issues in Diversity”, Oulu ülikool, Soomes

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