Hungarian University of Agriculture and Life Sciences

Role of functional traits in setting conservation priorities

DOI: 10.54598/006270

Hanny-Endrédi Anett

Gödöllő

2025

Doctoral school

name: Doctoral School of Biological Sciences

discipline: biological science

head: Dr. Nagy Zoltán
Professor, DSc
MATE
Department of Plant Physiology and Plant Ecology

Thesis leader(s): Dr. Nagy János György
Associate professor, PhD, habil.
MATE
Doctoral School of Biological Sciences

....
Approval by the Head of School

....
Approval of the thesis leader(s)

CONTENT

1. BACKGROUND AND OBJECTIVES

1.1. Introduction

Biodiversity and the services it provides are the basis of human well-being (Isbell et al., 2017), so its rapid loss can cause serious concern. Research suggests that both accelerating climate change and direct human impacts (e.g. habitat reduction, degradation, fragmentation, and over-exploitation of populations) are contributing significantly to this decline (Jaureguiberry et al., 2022; Malhi et al., 2020; Maxwell et al., 2016; Sala et al., 2000). These processes simultaneously drive changes at multiple levels of organisation, including significantly affecting community productivity and the species' relationships, phenology and distribution patterns (Parmesan & Yohe, 2003; Scheffers et al., 2016). This, in turn, may lead to significant species turnover and extinctions in many regions (Thuiller et al., 2005).

Conservation programmes seek to mitigate impacts in many places, but finite resources and time require prioritisation. Since a thorough understanding of the system to be protected is essential for developing an effective conservation strategy, research on the functioning, environmental responses, and threats of individual species and ecosystems is paramount (Standovár & Primack, 2001). Such case-specific research can be of great help in the conservation of a given species/ecosystem, but the alarmingly accelerating rate of biodiversity loss makes it increasingly urgent to synthesise our existing knowledge and use it to predict the sensitivity and optimal conservation strategy for species/ecosystems for which no specific research is yet available. Trait-based approaches, thinking beyond the traditional species concept, can help in this.

In trait-based research, species are replaced by their relevant functional traits that can be measured objectively at the level of individuals. This approach allows for the direct incorporation of biologically relevant information into different models and helps to generalise results by reducing their taxon- and ecosystem-dependence (Endrédi et al., 2018; McGill et al., 2006).

From an ecological point of view, the most important traits are functional traits related to the functioning of ecosystems: morphological, physiological, phenological and life-history traits that can directly or indirectly influence the fitness of individuals. These are traits related to growth, reproduction and survival (Violle et al., 2007), and either so-called response traits, which measure an organism's response to environmental changes, or effect traits, which determine the impact of an organism on ecosystem functioning (Lavorel & Garnier, 2002). Some traits (such as body size) can function as both, responding to the environment while influencing the function of individuals in the community (Gallé & Batáry, 2019).

Traits are now widely used in plant ecology and animal ecology. To prioritise conservation actions, researchers are developing models to predict the likely responses of species and communities to future environmental changes (Thuiller et al., 2008). However, such models require a large amount of high-quality trait data, which has necessitated the collection of species traits and led to the development of large trait databases. Although these databases have recently achieved unprecedented coverage (Kattge et al., 2020), there are still critical knowledge gaps. The characterisation of some traits (e.g., seed-related traits for plants (Jiménez-Alfaro et al., 2016; Saatkamp et al., 2019)) or taxa (e.g., invertebrates (Gallé & Batáry, 2019; Moretti et al., 2017) or rare species (Kattge et al., 2020)) is severely lacking, so for the time being the use of traits is limited.

1.2. Objectives

In my PhD thesis, I investigated how biological traits can help to set conservation priorities at the population, species and ecosystem levels. I investigated the question at different levels of organisation (population, species and ecosystem) and in different (terrestrial and marine) ecosystems. Numerous approaches (field data analysis, experiments and theoretical model analysis) were used, too. This variability in conservation targets and methods aimed to gain a broader picture of the conservation uses of traits. As the thesis comprises three widely divergent studies, I have organised the research into separate chapters by topic (progressing from population-level research to ecosystem-level research) and followed the usual structure only within each chapter. At the end of the thesis, I summarised the conclusions in a common discussion.

In the first study, we investigated the variation of vegetative and reproductive traits as a function of altitude in the local populations of a terrestrial orchid, red helleborine (*Cephalanthera rubra* (L.) Rich.). Since temperature and precipitation change with increasing altitude, this study may help understand how the studied species respond to climate change.

In the second study, I investigated the reproductive traits of endangered native fabaceous species in germination experiments. The primary aim of the research was to collect seed biology data on rare Hungarian species that are still endangered in Hungary despite long-standing legal protection to understand the reasons for their endangerment.

In the third study, leaving the conservation of terrestrial plant species aside, I used food web models of marine ecosystems to investigate how species' roles in food webs can be estimated and how functional traits can help us understand which groups occupy key positions in each ecosystem.

2. BIOLOGICAL TRAITS OF RED HELLEBORINE AS A FUNCTION OF ALTITUDE

2.1. Introduction

Over the last decades, several studies have confirmed that global warming is causing plant species to continuously migrate to higher latitudes and altitudes in search of new suitable habitats (Chen et al., 2011; Engler et al., 2011; Lenoir et al., 2008), making boreal and alpine species highly vulnerable (Thuiller et al., 2005). However, the future of plants that now live at lower latitudes/elevations is not always assured either: some species are unable to keep pace with change due to their slow dispersal (Urban, 2015) or because optimal dispersal pathways have been disrupted in landscapes fragmented by human activities (Krosby et al., 2010).

The movement of plant species can be further constrained by their interspecific relationships: faster-spreading competitors can significantly inhibit dispersal (Urban et al., 2012), but pollinators and mycorrhizal partners that respond differently to climate or habitat change can also affect species' adaptive success, especially for specialist species. (Bennett & Classen, 2020; Burkle et al., 2013; Rillig et al., 2002; Settele et al., 2016).

Terrestrial orchids are one of the most threatened plant groups, primarily due to habitat loss (Fay, 2018; Seaton et al.,2010), but they are also affected by climate change: the range of these species has also shifted towards the poles and higher regions (Barman & Devadas, 2013). Their vulnerability is significantly amplified by their complex life history strategies and unique relationships with pollinators and mycorrhizal fungal partners (Fay, 2018). Maintaining adequate fertilisation rates, which are highly dependent on pollinators, is the most critical for their survival (Tremblay et al., 2005). They may, therefore, be particularly vulnerable to the potential 'decoupling' from pollinators due to climate change, i.e. the phenomenon where the flowering period of plants and the emergence period of pollinators no longer co-occur due to different phenological responses to the changing climate. In addition, of course, changing climate can also directly affect the success of flowering and fruit maturation, pollinating insects (Hegland et al., 2009; Settele et al., 2016) or even mycorrhizal partners and their relationships (Bennett & Classen, 2020; Rillig et al., 2002).

2.2. Objectives

The research presented here aimed to get closer to understanding how native terrestrial orchids may respond to climatic changes. To investigate this, we compared growth-related (vegetative) and reproductive traits in four populations of red helleborine (*Cephalanthera rubra* (L.) Rich.) along an altitudinal gradient. The study questions were:

- How do the individuals' vegetative traits (height, number of leaves and leaf size) vary with altitude?
- How do their reproductive traits (number of flowers and fruits and the fertilisation rate) vary with altitude?
- How do the above-mentioned traits relate to each other (which react similarly or differently to the changing conditions)?

2.3. Material and methods

We studied four Hungarian populations at different altitudes: one on the Alföld (Jászfényszaru (103m)) and three in the Bükk Mountain: Kis-Oltár (361m), Bikk-bérce (533m) and Pongor-lyuk-tető (657m).

The populations live on brown forest soils created on calcareous bedrock. The average annual temperature at Jászfényszaru is 3-4°C higher (~11°C) than in the Bükk populations' habitat (7-8°C). The amount and distribution of precipitation show a high inter-annual variability. In the year of our study, two periods of higher precipitation were observed in late winter and early summer in the Jászfényszaru habitat. In comparison, there was also a third wet period in September in the Bükk area (MetNet, 2019).

The population of Jászfényszaru is located in a Euro-Siberian forest-steppe oak forest, where high densities of herbaceous and shrubby plants are typical. Canopy closure ranges between 75 and 90%. In contrast, the vegetation in the habitat of the Bükk populations is rocky beech forest, where canopy closure is above 90% and herbaceous and shrub cover is sparse, except the population in Kis-Oltár, where tree felling has temporarily improved light conditions in one-fifth of the habitat.

In 2018, two surveys were carried out in all populations. First, during the flowering period, May-June, we counted and marked all individuals (J: 100, KO: 22, BB: 85, PP: 27), then measured their height, leaf length and width and counted the number of leaves and flowers. The second time, in July-August, the number of fruits was counted.

Due to the different distribution of the measured variables, different analyses were performed to compare the populations: 1) log-transformed height and leaf size data were compared using one-way ANOVA; 2) negative binomial regression was used to compare the number of flowers and fruits, while 3) number of leaves was analysed using quasi-Poisson regression. Population pairs were then compared using Tukey's post-hoc tests.

2.4. Results and discussion

Although there was no consistent decrease in shoot length with increasing altitude, the plants in the Jászfényszaru habitat had significantly taller stems and larger leaves than the individuals in the Bükk Mountains. The proportion of flowering individuals decreased steadily upwards (Figure 1). The decreasing temperature with altitude may partly explain these. However, these traits may also have been influenced by the decrease in light levels here, as the canopy in the mountain populations is more closed.

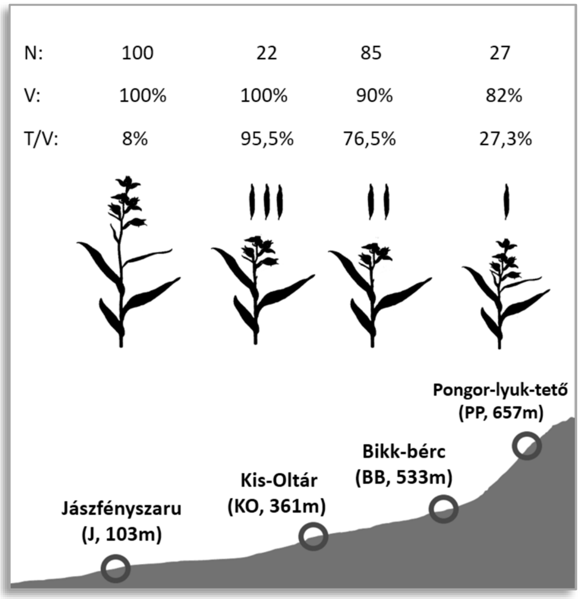

Figure 1. Traits of red helleborine along different altitudes. N= number of individuals in the populations, V= ratio of flowering individuals, T/V= Ratio of flowering individuals that also produced fruits. Schematic plants show the average heights and the number of leaves, flowers, and fruits in the populations.

Although there is a correlation between vegetative production and the probability of flowering, height and leaf area of rhizomatous or tuberous orchids may have a greater influence on the following year's flowering than in the current year (Bódis & Molnár, 2011; Janečková & Kindlmann, 2002). These results suggest that temperature and light in the two lowest populations were previously sufficient for all plants to flower. In contrast, the shadier habitat of the highest mountain populations probably did not provide sufficient energy for all plants to flower in the year of our study.

In terms of flower numbers, although the three lower habitats showed a slight decreasing pattern with altitude, the population at the highest altitude had more flowers per individual than expected.

The proportion of fruiting individuals also steadily decreased with altitude in the mountain habitat, but was much lower in the lowland habitat, with only 8% of flowering individuals fruiting compared to the 27-95% fertilisation rate in the mountain populations.

Non-nectar-producing, deceptive orchids are highly pollinator- and pollen-limited, and their reproductive success is generally low (Tremblay et al., 2005). Red helleborine is a food-deceptive orchid with flowers that mimic those of *Campanula spp*. (Newman et al., 2007; Nilsson, 1983) , and although the species is fully self-compatible, spontaneous self-pollination (autogamy) has not yet been observed (Tałałaj et al., 2017), so its reproductive success is strongly dependent on the presence and density of pollinators and bellflowers (Taura & Gudžinskas, 2024, 2025). The pollinator species observed so far are known to be strongly associated with bluebells, and the two *Chelostoma* bee species nest in standing deadwood, the presence of which can also strongly influence pollinator abundance (Claessens et al., 2015; Newman et al., 2007; Nilsson, 1983).

No bluebells have been found within a few kilometres of the habitat of our lowland population. Based on this, the number of potential pollinators in the area is probably very low. Although a more open canopy level results in higher irradiance, i.e. more energy, it also results in higher competition of herbaceous plants, which may reduce visibility, further reducing the likelihood of pollination. In such a habitat, a good strategy may be to be taller and have more flowers to attract attention among other herbaceous plants. Competition for a small number of pollinators may explain why only conspicuous, tall individuals with more flowers showed pollination success within the population (Kindlmann & Jersáková, 2006; Suetsugu et al., 2015), although this success was still far below that observed in upland populations. This low pollination rate may also lead to more frequent vegetative reproduction in the longer term. The higher frequency of vegetative reproduction may also be indicated by the fact that this population consisted of far more (100) individuals than the average population size (1-20 individuals) (Brzosko & Wróblewska, 2003) reported in the literature and our other populations.

In contrast, two species of bluebells occurred in high abundance near the mountain populations. Here, the stems of the helleborine specimens were shorter than in the lowland populations, and the number of flowering and fruiting specimens decreased with altitude. The reproductive success of the two lowest mountain populations was extremely high: 95-76% of flowering plants could produce at least one fruit, while on the Pongor-lyuk-tető, at the highest altitude, significantly fewer plants were fertilised. The vegetation and abundance of bluebells were similar in the three habitats, and herbaceous competition was low. Thus, the declining fertilisation rate may be due to decreasing pollinator abundance with altitude. This hypothesis may be supported by the fact that we already saw decreasing fertilization rates between the two lower populations. Furthermore, despite having a leaf area similar to the other upland populations, individuals of the highest population produced significantly more flowers than if they had struggled to attract pollinators as in the Jászfényszaru population.

The number of fruits per individual showed an inverse pattern than the number of flowers: the lowest and the highest populations, which on average produced the most flowers, had the lowest average number of fruits. Basically, in the case of deceptive species, neither the proportion of pollinated plants nor the number of fruits increases with flower number (Jersáková et al., 2006). For this reason, and because the establishment of flowers is so costly that the following year's vegetative shoots suffer from their establishment (Bódis & Molnár, 2011), increasing flower numbers to increase reproductive success is not an effective strategy in most cases. We also found that in the two populations with the highest fruit production, the size of inflorescences was intermediate, and the number of flowers was not related to either the probability of flowering or the proportion of flowers that were fertilised. In contrast, individuals in the lowest and highest altitude populations developed much larger inflorescences. This may have been at a greater cost to individuals in the high altitude population because of limitation of the light. However, it also had a greater benefit because although the probability of fertilisation did not increase with flower number, the number of flowers per individual was significantly higher than in the lowland population. Nevertheless, in both populations, the success in yielding was far below that of the other two populations.

2.5. Conclusions and suggestions

Overall, our research has shown that the variability in vegetative and reproductive traits along the altitudinal gradient can help us to understand not only the status of populations but also the strategy and vulnerability of the species. The results suggest that the generative reproduction of this species is mainly limited by its close relationship with pollinators, which makes it not very well adapted to the highest or the lowest habitats. The weather in the highest elevation area is likely to be unfavourable to the pollinators themselves. In contrast, in the lowest elevation area, the lack of bellflowers, which are the pollinators' preferred partners, and the higher flower competition reduces pollination rates. Based on this, the effect of climate change cannot be clearly predicted, and a study of the responses of bluebell species and specific pollinators to climate change would be required. In addition, it would be important to investigate whether other species also pollinate red helleborines, and to monitor plant population dynamics over several years to further refine the conclusions drawn by taking into account inter-annual relationships.

3. REPRODUCTIVE TRAITS OF ENDANGERED PLANTS AND THEIR CONSERVATIONAL IMPORTANCE

3.1. Introduction

Several studies have shown that rare species often perform important and vulnerable ecosystem functions (Lyons et al., 2005; Mouillot et al., 2013), as they often have unique combinations of functional traits in a given community (Jain et al., 2014). They can play a crucial role in stabilising food webs (Säterberg et al., 2019), and their presence can alsoenhance a community's resilience to invasions (Lyons & Schwartz, 2001). In other words, their role in ecosystem functioning and maintaining ecosystem services can be significant (Dee et al., 2019) compared to their abundance. However, they are more vulnerable to climate change, habitat loss, and disturbance, and their loss could contribute disproportionately to the current extinction crisis (Enquist et al., 2019; Pimm et al., 1988).

Effective in-situ (in-habitat) and ex-situ (out-of-habitat) conservation of rare plant species requires not only a thorough knowledge of populations and habitats but also a basic understanding of the life history characteristics associated with germination and seedling establishment, which can significantly influence population growth, stability and dispersal (Pence et al., 2022; Saatkamp et al., 2019). This knowledge is also essential for the effective reintroduction of rare species (Godefroid et al., 2011), and even more important for endangered annual plants, where regeneration from seeds is a key process due to their short life cycle.

However, these are the traits we know the least about, especially for rare, economically insignificant species. At the same time, a growing body of research shows that their knowledge can significantly contribute to understanding and predicting species' responses to environmental change (Jiménez-Alfaro et al., 2016; Saatkamp et al., 2019).

3.2. Objectives

The primary objective of the research presented here is to study three little-known, endangered annual fabaceous plant species, the Siberian vetch (*Vicia biennis* L.), the arrowleaf clover (*Trifolium vesiculosum* Savi.), and the Hungarian milkvetch (*Astragalus contortuplicatus* L.) to collect seed traits that are key to the establishment and persistence of populations. We also aimed to take advantage of trait-based approaches to compare known and newly collected trait data with known relationships in the literature and to use them to identify potential sources of species vulnerability and to understand their current demography and distribution. The main questions of the study were:

- What is the mass of seeds in local populations?
- What is the level of physical dormancy of the seeds of local populations?
- What is the germination capacity of the seeds of local populations?
- What is the potential lifespan of the seeds of the species? What type of seed bank do they have?

3.3. Material and methods

In the first half of our research, we investigated the weight, viability and dormancy of seeds collected from natural populations in germination experiments. For this purpose, we had five in-situ collected seed lots for the Siberian vetch, one for the arrowleaf clover and two for the Hungarian milkvetch. Before the germination tests, the weight of 3x20 seeds from each seed lot was weighed using an analytical scale. Where this number of seeds was unavailable, each seed was weighed individually. Then, half of the seed samples were individually hurt (scarified) with sandpaper to break any physical dormancy. The other half of the samples were germinated as a control. Germination was carried out in a greenhouse, in Petri dishes or soil, with each seed soaked in tap water for 24 hours beforehand. Seed water uptake (swelling) and germination were monitored for 30 days.

Then, in the second series of experiments, the potential longevity of seeds was investigated, mainly using seeds collected from ex-situ populations or herbarium sheets. For Siberian vetch, we germinated four lots of ex-situ seeds for 1-8 years and tested the germination of 7pcs of 1915 seeds collected from a herbarium sheet. For arrowleaf clover, one in-situ and three ex-situ seed lots were tested for germination over 1-6 years, while for Hungarian milkvetch, one in-situ and one ex-situ seed lot were germinated over 2-4 years, with an additional 60-62pcs 95-99-year-old herbarium-derived seeds. In this experiment, scarified seeds were germinated.

The germination and dormancy of different seed samples and the effect of seed weight on seed germination probability were compared using logistic regression and Chi-square or Fisher's exact test, while linear regression was used to compare the mean seed weights of in-situ seed samples.

3.4. Results and discussion

To summarize the results, seeds of Siberian vetch showed high viability (78-88% germination) and high physical dormancy (above 90%) in all populations studied, while seed weight varied significantly between years and populations. Nevertheless, the majority of seeds, regardless of population, reached the critical mass (~10mg) above which they were likely to germinate. Although the seeds can maintain viability beyond five years, their lifespan is not much more than five years (in dry storage).

Also, arrowleaf clover seeds showed high physical dormancy (above 74%) in all seed lots. Seeds germinated significantly better in Petri dishes than in soil and showed no significant reduction in viability at six years. The mean seed weight of the seed lots was also significantly different here but did not cause significant differences in germination rates.

The seeds of Hungarian milkvetch also have a high viability (90-96% germination) and a physical dormancy above 91%. After 94 years of dry storage, both dormancy and germination are significantly reduced, but the seeds are still able to germinate after 99 years.

The high seed viability of all three species suggests that the populations are in good condition, with no signs of inbreeding.

Although dormancy is an important part of the risk-distribution strategy in short-lived plant species (Childs et al., 2010; Cohen, 1966; Pake & Venable, 1996), the high levels of dormancy commonly observed in these species suggest that they are adapted to highly variable and unpredictable environment (Childs et al., 2010; Cohen, 1966).

Comparing our results with literature data, we can state that the phylogenetic relationships, seed masses, life histories and habitat preferences all support the hypothesis that the three species we studied all have long term persistent seed bank, and the expected life span pf the seeds are not much more than 5-10 years for the Siberian vetch, probably slightly more for the arrowleaf clover, and more than 100 years for the Hungarian milkvetch.

Our results may be of great conservation importance because they show that the native populations of the studied species, despite their small and highly variable sizes, produce seeds with good germination capacity, and are well adapted to the variable environment, as high dormancy can spread their germination and the seeds can preserve their viability over years, waiting for the optimal conditions for germination.

3.5. Conclusions and suggestions

Our experiments have shown that measuring and comparing species traits with other species' can help set conservation priorities. Summarising the conservation-relevant characteristics of the three species, we can see that:

1) All three species produce good quality, viable seeds in all studied populations, so the populations do not show signs of inbreeding.
2) All three species can have a long-term persistent seed bank containing a high proportion of dormant seeds, potentially providing seedlings for up to a decade in the case of Siberian vetch, possibly longer in the case of arrowleaf clover, and up to 100 years in the case of Hungarian milkvetch,
3) The most sensitive period of the arrowleaf clover's life is the period following autumn germination when it has a high rainfall requirement and low competitive ability. In contrast, Siberian vetch and Hungarian milkvetch require adequate soil moisture and reduced competition before flowering, in summer.
4) In all three species, individuals that reach flowering can be easily fertilized even far from their natural habitat, suggesting no specific pollinator requirements. They can also produce large numbers of seeds.
5) In Hungarian milkvetch, dispersion by water and animals can help the seeds travel greater distances. In the case of Siberian vetch and arrowleaf clover, although their hard-seeded, non-toxic seeds have the potential for endozoochorous dispersal, no such dispersal is known to date. Thus, their dispersion may be limited and slow, hindering their ability to respond to climate change at an appropriate pace.

According to regional climate models (Lakatos et al., 2018), decreasing annual precipitation and increasing annual mean temperature are expected to reduce soil moisture and increase the frequency and duration of droughts. Precipitation deficits will affect summers when the studied species are in their pre-flowering period, and thus the particularly sensitive Siberian vetch and Hungarian milkvetch will be more severely affected. These species may move closer to wetter areas if their population movements are not restricted. At the same time, they can wait in the soil seed bank for a long period for the increasingly rare, wetter years and refill the seed bank in a single year. In this respect, the Siberian vetch is the most vulnerable species because its seeds lose their ability to germinate sooner, so if the frequency of wet years falls below a threshold, the seed banks may be depleted, and these small western peripheral populations may disappear.

The most important question is the species' ability to 'escape' the changing climate, i.e. how far and how fast their seeds can spread. Even if dispersal is not limited, the actual status of populations and the extent of their vulnerability will not be known for years because of high dormancy. In order to assess this, it would be advisable to carry out extensive, targeted research to determine the status of seed banks. In addition, conservationists can carry out seed sowing in areas considered optimal to help dispersion. However, the impact of this - whether stable populations have been established - will also take years to be seen.

4. BIOLOGICAL TRAITS IN AQUATIC FOOD WEB MODELS

4.1. Introduction

Many interactions between living organisms link them together into functioning communities. Since the trophic (feeding) relationships are among the most important ones in determining the structure of the communities, food web models can be useful tools for understanding community functioning and predicting future changes (Thompson et al., 2012).

The strength of these models is that they take into account not only direct relationships between species but also indirect effects across species; their use is, therefore, becoming increasingly common (Wootton, 2002). They are suitable for quantifying ecological processes such as the effects of invasion and disturbance (Coll et al., 2011; Woodward & Hildrew, 2001) or productivity (Wang & Brose, 2018). Furthermore, they can also be used to investigate important conservation questions such as which species/trophic groups have the greatest impact on other community members - i.e. which are the key groups whose loss would significantly disrupt community functioning (Jordan et al., 2006). This latter can also help prioritise conservation actions.

Ecological roles and position in food webs are not unrelated (Luczkovich et al., 2003), so it is not surprising that since the earliest attempts to identify key species of communities (Paine, 1969), their position in food webs is a main question (Mills et al., 1993; Power et al., 1996). Various simple hypotheses (e.g., keystone species are always top predators) have not proved to be globally valid, so it is worthwhile to investigate the issue using more complex approaches. Although the relative importance of organisms varies over time and space, analysis of a large database can provide general insights into which organisms play key roles in the networks.

Recently, a large number of food web models have been developed, especially for marine ecosystems (Colléter et al., 2015). However, these models are case-specific: they focus on different issues, include different trophic groups and measure their importance in different ways, making their results difficult to compare. At the same time, there is a growing need to explore cross-ecosystem patterns. A trait-based approach can help: characterising trophic groups by functional traits can make results more general, food webs more comparable, and models more predictive.

4.2. Objectives

In this research, we sought to answer the question of to what extent biological traits can be used to explain and predict which species play key roles in ecosystems. Since only a few food webs are constructed in a standard way in the very heterogeneous terrestrial communities, we used the numerous food web models developed in a comparable way for marine ecosystems to answer our question. The main questions of the study were:

- How do we define key species based on their position (topology) in the network? In other words, how do the many approaches that have been developed to quantify the impact of groups relate to each other?
- To what extent do the easily identifiable traits relevant in marine ecosystems (size, mobility and habitat type) explain the impact and topological importance of trophic groups in the food web?

4.3. Material and methods

We used 92 individual networks from the food webs collected by Heymans et al. (2014). They vary in resolution (9-68 clusters) and are originated from five continents and five different ecosystem types. However, they were all constructed using the same methodology, the Ecopath with Ecosim (Ewe) modelling approach (Christensen & Walters, 2004; Heymans et al., 2016).

Non-living and isolated components were removed from the models before the analyses, and, where it was necessary, a loop-free version of the models was created to calculate hierarchical indices.

The role of trophic groups was estimated by quantifying their topological importance based on their position in the network. To do this, we used 18 different, commonly used topological indices that estimate species' impact using different approaches.

Functional groups were then assigned to three categorical traits: habitat (with two subcategories), mobility (with four subcategories) and size (with nine subcategories). Trait data were collected from more than 15 different databases and articles.

The relationship between topological indices was investigated using metric (principal component analysis (PCA) and hierarchical clustering) and ordinal (Spearman rank correlation and non-metric multidimensional scaling (NMDS)) methods. The independence of the three traits was tested using Chi-square test and Fisher's exact test with simulated p-values. Finally, the relationship between topological indices and functional traits was analysed using linear mixed models. In the models, individual indices were the response variables, while traits were included as fixed effects and networks as random effects. Before building the models, ten indices had to be transformed due to their left-skewed distribution and each index was standardised within its network.

4.4. Results and discussion

According to our results, the studied 18 topological indices can be grouped into five distinct clusters, each identifying different species as keystone species. The grouping is well explained by the way each index takes into account the strength and direction of interactions. This is consistent with the results of previous small-scale studies (Jordán et al., 2006, 2007; Lai et al., 2015).

Regarding traits, the topological importance of organisms with different mobility differed significantly in 82% of the comparisons. This trait best explains the topological importance predicted by the top-down (estimating predation effects) and weighted (estimating the role in material flow) indices. Body length significantly explained the importance predicted by the indices in almost 70% of the comparisons and was related to index values similarly to mobility. In contrast, habitat explained topological importance well in only 50% of the cases, although it worked well for all centrality indices.

As the three traits are not independent of each other, the results suggests that 1) hierarchical indices ranking by predation effects identify fast-moving, large (>1m) species as keystone species, while 2) indices ranking by bottom-up effects and energy fluxes highlight the importance of passively drifting groups, that are smaller than 1 cm. 3) In addition, medium-sized, 1-10 cm, slow-moving, benthic species may also occupy a central position in the network (based on centrality indices): their direct effects and unique position in connecting others make them stand out.

4.5. Conclusions and suggestions

In our studies of marine food webs, we have found that using biological traits can help us notice robust patterns across ecosystems and better understand the biological underpinnings of our mathematical methods.

The indices we studied can be grouped into distinct clusters, which estimate the importance and the role of organisms through different functions:

- Centrality indices estimate the direct and short-term indirect effects of species based on the presence/absence of feeding relationships. They highlight groups with the greatest direct impact (e.g., DC) or those important in linking different parts of the network (e.g., BC).

- Weighted indices look for the groups through which most matter/energy flows (short or medium term), so their role in the matter/energy cycle is essential. Although these are highly informative indices, they require accurate knowledge of the interspecific material/energy fluxes, which is often unavailable or uncertain, and this can strongly affect the reliability and usefulness of these indices.
- Hierarchical indices are designed to analyse highly structured networks such as food webs. They can estimate the overall predation and resource effects of groups and decouple these two effects to help answer specific questions.

Based on this, we suggest using several (ideally 1-1 from each index cluster) complementary indices at the same time when searching for key species, which can help highlight all important groups.

The aim of our research was to link theoretical, network-based indicators of ecological role with more practical, ecologically relevant traits. Although exploring this link can help to ensure that theoretical models can provide real support for practical conservation, many questions remain to be answered before they can be applied. For example, it would be important to investigate what other traits might be potentially important in aquatic ecosystems and how the relationships between indices and traits depend on ecosystem type and depth.

Our research has shown that even simple, descriptive traits can successfully complement food web research, but combining the right traits would bring us even closer to understanding the ecological role and importance of groups. Such theoretical research could be greatly aided by the creation and expansion of large, standardized food web and trait databases. And new, increasingly sophisticated algorithms (e.g. machine learning) can help in quantitative analysis and uncovering hidden patterns. Thus, in the future, trait-based analyses have the potential to offer more than *in silico* rediscovery of classical biological knowledge (Endrédi et al., 2018).

5. DISCUSSION AND CONCLUSIONS

In this thesis, I investigated how the use of biological traits can help us understand the conservational status of populations, species and ecosystems and to set conservation priorities. I have explored the question at different levels of organisation (population, species and ecosystem), in different ecosystems (terrestrial and marine), and using different methods (field data analysis, experiments and theoretical model analysis) to gain a broader picture of the potential uses of traits.

According to Gallagher et al. (2021), conservation practice consists of five major steps: 1) assessing risk/sensitivity; 2) designing management strategies; 3) prioritising interventions; 4) spatially coordinating interventions; and 5) monitoring and evaluating the impact of interventions. The authors illustrate with real examples that biological traits can be of great help in each of these steps.

Our research is related to the first three points. In the case of red helleborine, we assessed the species' sensitivity to climatic and vegetation conditions (point 1), in the case of the endangered fabaceous species we used seed traits to gather data to refine conservation strategies (point 2), and in the case of food webs we used biological traits to answer questions about which groups in marine communities are key in protecting system functioning (point 3). In the first two cases, we measured the traits we considered important ourselves and then compared them between populations or species, thus, we could work with more accurate and reliable data. However, this is a more time-consuming and costly approach and still requires knowledge of trait correlations from the literature to interpret the results and draw conclusions.

Although most ecological research using traits today still uses species-level averaged trait values, it should be taken into account that within-species trait variability is the basis of adaptation (Moran et al, 2016), so knowledge of this is key to understanding how individual taxa will respond to environmental change

(Bolnick et al., 2011; Westerband et al., 2021). For this reason, it is important to have as many population-level trait measurements as possible and to ensure that our models can take these into account (Funk et al., 2017; Moran et al., 2016; Westerband et al., 2021). We also found different trait distributions in populations of red helleborine in different environments, which highlighted important relationships and helped us to understand that, although the species has a relatively wide tolerance for climatic and light conditions, its close biotic interactions make it potentially sensitive to climate change. Thus, to predict the future distribution of populations, the sensitivity of its interaction network to climate change needs to be assessed.

Although the best way to answer questions appropriate to the conservation objective is to measure case-specific characteristics, this is not always feasible. In many cases, experiments or field data collection may be too risky/disruptive for protected species, so consideration should be given to designing a conservation strategy based on available data from species with similar ecological traits. It is also impossible to measure all species' functional traits to compare food webs in different ecosystems, so it is particularly important to rely on existing data. Suppose a large number of measurements are available for ecologically similar species, and the traits selected are appropriate to the question. In that case, the analysis can provide reliable results and be more cost-effective than research limited to experimental and field data collection (Gallagher et al., 2021). However, this requires databases with sufficient coverage, accuracy and reliability. Although trait databases have recently achieved unprecedented coverage (e.g. Kattge et al., 2020), there are still critical knowledge gaps. Among plants, in particular, trait data for rare species are missing (Kattge et al., 2020), and among traits, seed-related properties− except seed mass (Jiménez-Alfaro et al., 2016; Saatkamp et al., 2019) are surprisingly underrepresented, even though these traits have a major influence on species dispersal, establishment and persistence (Jiménez-Alfaro et al., 2016), and are among the most important plant traits from a conservation perspective. In the case of animals, in particular, invertebrate taxa are data-poor (Gallé & Batáry, 2019; Moretti et al., 2017). Thus, an important task for future research is to expand the trait databases for unknown species and functional traits (Kremer et al., 2017; Moretti et al., 2017) and preferably map also the within-species variability of traits (Funk et al., 2017; Westerband et al., 2021). Another task is to develop standardised protocols for the use of traits. The latter has recently been increasingly exemplified in conservation (Gallagher et al., 2021). It is already apparent that functional traits can help, for example, in the designation of conservation areas (Miatta et al., 2021), habitat restoration (Carlucci et al., 2020; Clark et al., 2012) and in estimating species invasion potential (Funk et al., 2016; Mathakutha et al., 2019) or sensitivity (Fordham, 2024; González-Suárez et al., 2013). Thus, their use in setting conservation priorities is expected to be a major focus in the future.

6. NEW SCIENTIFIC RESULTS

In our research, we investigated the use of biological traits to answer conservation questions at three different levels of organisation.

In the first study, we investigated vegetative and generative traits of red helleborine at different altitudes to infer its climate sensitivity. Our main finding is that the vegetation and climatic conditions of the habitat affect reproductive success mostly indirectly, probably through pollinators, strongly limiting generative reproduction in some populations.

In the second study, the seed characteristics of endangered native fabaceous species, the Siberian vetch, the arrowleaf clover and the Hungarian milkvetch, were investigated to understand the reasons for their endangerment. We have shown that

- seeds of all three species show high viability and physical dormancy,
- the seed masses of both the Siberian vetch and the arrowleaf clover show great variation in different populations,
- in Siberian vetch, seed weight affects germination more than in arrowleaf clover, but above 10 mg seed weight they are more likely to germinate,
- the seeds of the Siberian vetch have a lifespan of not much more than five years,
- the arrowleaf clover seeds have not lost their ability to germinate within six years,
- and the seeds of Hungarian milkvetch can germinate after 99 years.

In the third study, we analysed food web models in marine ecosystems to see how functional traits can help us understand which species occupy key positions in each ecosystem. We have shown that

- indices developed to search for key species can be grouped into five groups, which estimate the importance of species through different biological functions,
- our study was the first to quantify and confirm through a large-scale, cross-ecosystem statistical analysis that the size and mobility of species provide a good estimate of their impact on the community:
  - fast-moving, large species control the numbers of others while
  - passively drifting, small groups provide the material and energy to the community and
  - medium-sized, slow-moving, benthic species have a unique position and an important linking role in the network.

7. REFERENCES

Barman, D., & Devadas, R. (2013). Climate change on orchid population and conservation strategies: a review. *Journal of Crop and Weed*, *9*(2), 1–12.

Bennett, A. E., & Classen, A. T. (2020). Climate change influences mycorrhizal fungal–plant interactions, but conclusions are limited by geographical study bias. *Ecology, 101*(4), 1–11. https://doi.org/10.1002/ecy.2978

Bódis, J., & Molnár, V. A. (2011). Az európai orchideák életmenete és populációdinamikája - áttekintés a Magyarország Orchideáinak Atlasza című kötethez. *Kitaibelia, 16*(1–2), 37–56. http://kitaibelia.unideb.hu/articles/Kitaibelia_vol1612_p37-56.pdf

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C., & Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, *26*(4), 183–192. https://doi.org/10.1016/j.tree.2011.01.009

Brzosko, E., & Wróblewska, A. (2003). Genetic variation and clonal diversity in island Cephalanthera rubra populations from the Biebrza National Park, Poland. *Botanical Journal of the Linnean Society*, *143*(1), 99–108. https://doi.org/10.1046/j.1095-8339.2003.00201.x

Burkle, L. A., Marlin, J. C., & Knight, T. M. (2013). Plant-pollinator interactions over 120 years: Loss of species, co-occurrence, and function. *Science*, *340*(6127), 1611–1615. https://doi.org/10.1126/science.1232728

Carlucci, M. B., Brancalion, P. H. S., Rodrigues, R. R., Loyola, R., & Cianciaruso, M. V. (2020). Functional traits and ecosystem services in ecological restoration. *Restoration Ecology*, *28*(6), 1372–1383. https://doi.org/10.1111/rec.13279

Chen, I.-C., Hill, J. K., Ohlemuller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, *333*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Childs, D. Z., Metcalf, C. J. E., & Rees, M. (2010). Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1697), 3055–3064. https://doi.org/10.1098/rspb.2010.0707

Christensen, V., & Walters, C. J. (2004). Ecopath with Ecosim: Methods, capabilities and limitations. *Ecological Modelling*, *172*(2–4), 109–139. https://doi.org/10.1016/j.ecolmodel.2003.09.003

Claessens, J., Beentjes, K. K., Heijerman, T., Miller, J., & Gravendeel, B. (2015). Beobachtungen von Miarus campanulae als Bestäuber von Cephalanthera rubra Keywords. *Journal Europäischer Orchideen*, *47*(1), 77–87.

Clark, D. L., Wilson, M., Roberts, R., Dunwiddie, P. W., Stanley, A., & Kaye, T. N. (2012). Plant traits – a tool for restoration? *Applied Vegetation Science*, *15*(4), 449–458. https://doi.org/10.1111/j.1654-109X.2012.01198.x

Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology*, *12*(1), 119–129. https://doi.org/10.1016/0022-5193(66)90188-3

Coll, M., Schmidt, A., Romanuk, T., & Lotze, H. K. (2011). Food-Web structure of seagrass communities across different spatial scales and human impacts. *PLoS ONE*, *6*(7). https://doi.org/10.1371/journal.pone.0022591

Colléter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D., & Christensen, V. (2015). Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. *Ecological Modelling*, *302*, 42–53. https://doi.org/10.1016/j.ecolmodel.2015.01.025

Dee, L. E., Cowles, J., Isbell, F., Pau, S., Gaines, S. D., & Reich, P. B. (2019). When Do Ecosystem Services Depend on Rare Species? *Trends in Ecology and Evolution*, *34*(8), 746–758. https://doi.org/10.1016/j.tree.2019.03.010

Endrédi, A., Jordán, F., & Abonyi, A. (2018). Trait-based paradise – or only feeding the computer with biology? *Community Ecology*, *19*(3), 319–321. https://doi.org/10.1556/168.2018.19.3.13

Engler, R., Randin, C. F., Thuiller, W., Dullinger, S., Zimmermann, N. E., Araújo, M. B., Pearman, P. B., Le Lay, G., Piedallu, C., Albert, C. H., Choler, P., Coldea, G., De Lamo, X., Dirnböck, T., Gégout, J. C., Gómez-García, D., Grytnes, J. A., Heegaard, E., Høistad, F., … Guisan, A. (2011). 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, *17*(7), 2330–2341. https://doi.org/10.1111/j.1365-2486.2010.02393.x

Enquist, B. J., Feng, X., Boyle, B., Maitner, B., Newman, E. A., Jørgensen, P. M., Roehrdanz, P. R., Thiers, B. M., Burger, J. R., Corlett, R. T., Couvreur, T. L. P., Dauby, G., Donoghue, J. C., Foden, W., Lovett, J. C., Marquet, P. A., Merow, C., Midgley, G., Morueta-Holme, N., … McGill, B. J. (2019). The commonness of rarity: Global and future distribution of rarity across land plants. *Science Advances*, *5*(11), 1–14. https://doi.org/10.1126/sciadv.aaz0414

Fay, M. F. (2018). Orchid conservation: how can we meet the challenges in the twenty-first century? *Botanical Studies*, *59*(1). https://doi.org/10.1186/s40529-018-0232-z

Fordham, D. A. (2024). Identifying species traits that predict vulnerability to climate change. *Cambridge Prisms: Extinction*, *2*, e21. https://doi.org/10.1017/ext.2024.24

Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., Laughlin, D. C., Sutton-Grier, A. E., Williams, L., & Wright, J. (2017). Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews*, *92*(2), 1156–1173. https://doi.org/10.1111/brv.12275

Funk, J. L., Standish, R. J., Stock, W. D., & Valladares, F. (2016). Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems. *Ecology*, *97*(1), 75–83. https://doi.org/10.1890/15-0974.1

Gallagher, R. V., Butt, N., Carthey, A. J. R., Tulloch, A., Bland, L., Clulow, S., Newsome, T., Dudaniec, R. Y., & Adams, V. M. (2021). A guide to using species trait data in conservation. *One Earth*, *4*(7), 927–936. https://doi.org/10.1016/j.oneear.2021.06.013

Gallé, R., & Batáry, P. (2019). Trait-based paradise — about the importance of real functionality. *Community Ecology*, *20*(3), 314–316. https://doi.org/10.1556/168.2019.20.3.11

Godefroid, S., Piazza, C., Rossi, G., Buord, S., Stevens, A. D., Aguraiuja, R., Cowell, C., Weekley, C. W., Vogg, G., Iriondo, J. M., Johnson, I., Dixon, B., Gordon, D., Magnanon, S., Valentin, B., Bjureke, K., Koopman, R., Vicens, M., Virevaire, M., & Vanderborght, T. (2011). How successful are plant species reintroductions? *Biological Conservation*, *144*(2), 672–682. https://doi.org/10.1016/j.biocon.2010.10.003

González-Suárez, M., Gómez, A., & Revilla, E. (2013). Which intrinsic traits predict vulnerability to extinction depends on the actual threatening processes. *Ecosphere*, *4*(6), 1–16. https://doi.org/10.1890/ES12-00380.1

Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A.-L., & Totland, Ø. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters*, *12*(2), 184–195. https://doi.org/10.1111/j.1461-0248.2008.01269.x

Heymans, J. J., Coll, M., Libralato, S., Morissette, L., & Christensen, V. (2014). Global patterns in ecological indicators of marine food webs: a modelling approach. *PloS One*, *9*(4), e95845. https://doi.org/10.1371/journal.pone.0095845

Heymans, J. J., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., & Christensen, V. (2016). Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecological Modelling*, *331*, 173–184. https://doi.org/10.1016/j.ecolmodel.2015.12.007

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., MacE, G. M., Wardle, D. A., O'Connor, M. I., Duffy, J. E., Turnbull, L. A., Thompson, P. L., & Larigauderie, A. (2017). Linking the influence and dependence of people on biodiversity across scales. *Nature*, *546*(7656), 65–72. https://doi.org/10.1038/nature22899

Jain, M., Flynn, D. F. B., Prager, C. M., Hart, G. M., DeVan, C. M., Ahrestani, F. S., Palmer, M. I., Bunker, D. E., Knops, J. M. H., Jouseau, C. F., & Naeem, S. (2014). The importance of rare species: A trait-based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. *Ecology and Evolution*, *4*(1), 104–112.

https://doi.org/10.1002/ece3.915

Janečková, P., & Kindlmann, P. (2002). Key factors affecting shoot growth and flowering performance of Dactylorhiza fuchsii. In P. Kindlmann, J. H. Williams, & D. F. Whigham (Eds.), *Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations* (pp. 99–113). Backhuys Publishers.

Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D. E., Coscieme, L., Golden, A. S., Guerra, C. A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., & Purvis, A. (2022). The direct drivers of recent global anthropogenic biodiversity loss. *Science Advances*, *8*, 9982. https://www.science.org

Jersáková, J., Johnson, S. D., & Kindlmann, P. (2006). Mechanisms and evolution of deceptive pollination in orchids. *Biological Reviews*, *81*(02), 219. https://doi.org/10.1017/S1464793105006986

Jiménez-Alfaro, B., Silveira, F. A. O., Fidelis, A., Poschlod, P., & Commander, L. E. (2016). Seed germination traits can contribute better to plant community ecology. *Journal of Vegetation Science*, *27*(3), 637–645. https://doi.org/10.1111/jvs.12375

Jordán, F., Benedek, Z., & Podani, J. (2007). Quantifying positional importance in food webs: A comparison of centrality indices. *Ecological Modelling*, *205*(1–2), 270–275. https://doi.org/10.1016/j.ecolmodel.2007.02.032

Jordán, F., Liu, W., & Davis, A. J. (2006). Topological keystone species: measures of positional importance in food webs. *Oikos*, *112*(3), 535–546. https://doi.org/10.1111/j.0030-1299.2006.13724.x

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar C, C., Aleixo, I., Ali, H., … Wirth, C. (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, *26*(1), 119–188. https://doi.org/10.1111/gcb.14904

Kindlmann, P., & Jersáková, J. (2006). Effect of floral display on reproductive success in terrestrial orchids. *Folia Geobotanica*, *41*(1), 47–60. https://doi.org/10.1007/BF02805261

Kremer, C. T., Williams, A. K., Finiguerra, M., Fong, A. A., Kellerman, A., Paver, S. F., Tolar, B. B., & Toscano, B. J. (2017). Realizing the potential of trait-based aquatic ecology: New tools and collaborative approaches. *Limnology and Oceanography*, *62*(1), 253–271. https://doi.org/10.1002/lno.10392

Krosby, M., Tewksbury, J., Haddad, N. M., & Hoekstra, J. (2010). Ecological Connectivity for a Changing Climate. *Conservation Biology*, *24*(6), 1686–1689. https://doi.org/10.1111/j.1523-1739.2010.01585.x

Lai, S., Liu, W., & Jordán, F. (2015). A trophic overlap-based measure for species uniqueness in ecological networks. *Ecological Modelling*, *299*, 95–101. https://doi.org/10.1016/j.ecolmodel.2014.12.014

Lakatos, M., Bihari, Z., Hoffmann, L., Izsák, B., Kircsi, A., & Szentimrey, T. (2018). *Observed climate change in Hungary 1901-2016 [in Hungarian]*. OMSZ - Hungarian Meteorological Service Webpage. https://www.met.hu/eghajlat/eghajlatvaltozas/megfigyelt_valtozasok/Magyarorszag/

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, *16*(5), 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lenoir, J., Gégout, J. C., Marquet, P. A., De Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, *320*(5884), 1768–1771. https://doi.org/10.1126/science.1156831

Luczkovich, J. J., Borgatti, S. P., Johnson, J. C., & Everett, M. G. (2003). Defining and Measuring Trophic Role Similarity in Food Webs Using Regular Equivalence. *Journal of Theoretical Biology*, *220*(3), 303–321. https://doi.org/10.1006/jtbi.2003.3147

Lyons, K. G., Brigham, C. A., Traut, B. H. H., & Schwartz, M. W. (2005). Rare species and ecosystem functioning. *Conservation Biology*, *19*(4), 1019–1024. https://doi.org/10.1111/j.1523-1739.2005.00106.x

Lyons, K. G., & Schwartz, M. W. (2001). Rare species loss alters ecosystem function - invasion resistance. *Ecology Letters*, *4*(4), 358–365. https://doi.org/10.1046/j.1461-0248.2001.00235.x

Malhi, Y., Franklin, J., Seddon, N., Solan, M., Turner, M. G., Field, C. B., & Knowlton, N. (2020). Climate change and ecosystems: Threats, opportunities and solutions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1794). https://doi.org/10.1098/rstb.2019.0104

Mathakutha, R., Steyn, C., le Roux, P. C., Blom, I. J., Chown, S. L., Daru, B. H., Ripley, B. S., Louw, A., & Greve, M. (2019). Invasive species differ in key functional traits from native and non-invasive alien plant species. *Journal of Vegetation Science*, *30*(5), 994–1006. https://doi.org/10.1111/jvs.12772

Maxwell, S., Fuller, R., Brooks, T., & Watson, J. (2016). The ravages of guns,nets and bulldozers. *Nature*, *536*, 143–145. www.iucnredlist.org

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, *21*(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002

MetNet. (2019). *MetNet*. https://www.metnet.hu/

Miatta, M., Bates, A. E., & Snelgrove, P. V. R. (2021). Incorporating Biological Traits into Conservation Strategies. *Annual Review of Marine Science*, *13*(January), 421–443. https://doi.org/10.1146/annurev-marine-032320-094121

Mills, L. S., Soulé, M. E., & Doak, D. F. (1993). The Keystone-Species Concept in Ecology and Conservation. *BioScience*, *43*(4), 219–224. https://doi.org/10.2307/1312122

Moran, E. V., Hartig, F., & Bell, D. M. (2016). Intraspecific trait variation across scales: Implications for understanding global change responses. *Global Change Biology*, *22*(1), 137–150. https://doi.org/10.1111/gcb.13000

Moretti, M., Dias, A. T. C., de Bello, F., Altermatt, F., Chown, S. L., Azcárate, F. M., Bell, J. R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J. P., Ellers, J., & Berg, M. P. (2017). Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, *31*(3), 558–567. https://doi.org/10.1111/1365-2435.12776

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C. E. T., Renaud, J., & Thuiller, W. (2013). Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. *PLoS Biology*, *11*(5), e1001569. https://doi.org/10.1371/journal.pbio.1001569

Newman, R. D., Showler, A. J., Harvey, M. C., & Showler, D. A. (2007). Hand pollination to increase seed-set of red helleborine Cephalanthera rubra in the Chiltern Hills, Buckinghamshire, England. In *Conservation Evidence* (Vol. 4). http://www.conservationevidence.com/ViewEntry.asp?ID=961www.ConservationEvidence.com

Nilsson, L. A. (1983). Mimesis of bellflower (Campanula) by the red helleborine orchid Cephalanthera rubra. *Nature*, *305*(5937), 799–800. https://doi.org/10.1038/305799a0

Paine, R. T. (1969). The Pisaster-Tegula Interaction: Prey Patches, Predator Food Preference, and Intertidal Community Structure. *Ecology*, *50*(6), 950–961. https://doi.org/10.2307/1936888

Pake, E., & Venable, D. L. (1996). Seed Banks in Desert Annuals : Implications for Persistence and Coexistence in Variable Environments. *Ecology*, *77*(5), 1427–1435.

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

Pence, V. C., Meyer, A., Linsky, J., Gratzfeld, J., Pritchard, H. W., Westwood, M., & Bruns, E. B. (2022). Defining exceptional species—A conceptual framework to expand and advance ex situ conservation of plant diversity beyond conventional seed banking. *Biological Conservation*, *266*, 109440. https://doi.org/10.1016/j.biocon.2021.109440

Pimm, S. L., Jones, H. L., & Diamond, J. (1988). On the Risk of Extinction. *The American Naturalist*, *132*(6), 757–785. https://www.jstor.org/stable/2462261

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., Castilla, J. C., Lubchenco, J., & Paine, R. T. (1996). Challenges in the Quest for Keystones. *BioScience*, *46*(8), 609–620. https://doi.org/10.2307/1312990

Rillig, M. C., Treseder, K. K., & Allen, M. F. (2002). *Global Change and Mycorrhizal Fungi*. *October 2014*, 135–160. https://doi.org/10.1007/978-3-540-38364-2_6

Saatkamp, A., Cochrane, A., Commander, L., Guja, L. K., Jimenez-Alfaro, B., Larson, J., Nicotra, A., Poschlod, P., Silveira, F. A. O., Cross, A. T., Dalziell, E. L., Dickie, J., Erickson, T. E., Fidelis, A., Fuchs, A., Golos, P. J., Hope, M., Lewandrowski, W., Merritt, D. J., … Walck, J. L. (2019). A research agenda for seed-trait functional ecology. *New Phytologist*, *221*(4), 1764–1775. https://doi.org/10.1111/nph.15502

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E. L., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global Biodiversity Scenarios for the Year 2100. *Source: Science, New Series*, *287*(5459), 1770–1774. http://www.jstor.org/stable/3074591

Säterberg, T., Jonsson, T., Yearsley, J., Berg, S., & Ebenman, B. (2019). A potential role for rare species in ecosystem dynamics. *Scientific Reports*, *9*(1), 11107. https://doi.org/10.1038/s41598-019-47541-6

Scheffers, B. R., De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., Butchart, S. H. M., Pearce-Kelly, P., Kovacs, K. M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W. B., Martin, T. G., Mora, C., Bickford, D., & Watson, J. E. M. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, *354*(6313). https://doi.org/10.1126/science.aaf7671

Seaton, P. T., Hu, H., Perner, H., & Pritchard, H. W. (2010). Ex situ conservation of Orchids in a warming world. *Botanical Review*, *76*(2), 193–203. https://doi.org/10.1007/s12229-010-9048-6

Settele, J., Bishop, J., & Potts, S. G. (2016). Climate change impacts on pollination. *Nature Plants*, *2*(7). https://doi.org/10.1038/NPLANTS.2016.92

Standovár, T., & Primack, R. (2001). *A természetvédelmi biológia alapjai*. Nemzeti Tankönyvkiadó.

Suetsugu, K., Naito, R. S., Fukushima, S., Kawakita, A., & Kato, M. (2015). Pollination system and the effect of inflorescence size on fruit set in the deceptive orchid Cephalanthera falcata. *Journal of Plant Research*, *128*(4), 585–594. https://doi.org/10.1007/s10265-015-0716-9

Tałałaj, I., Ostrowiecka, B., Włostowska, E., Rutkowska, A., & Brzosko, E. (2017). The ability of spontaneous autogamy in four orchid species: Cephalanthera rubra, Neottia ovata, Gymnadenia conopsea, and Platanthera bifolia. *Acta Biologica Cracoviensia Series Botanica*, *59*(2), 51–61. https://doi.org/10.1515/abcsb-2017-0006

Taura, L., & Gudžinskas, Z. (2024). What Factors Determine the Natural Fruit Set of Cephalanthera longifolia and Cephalanthera rubra? *Diversity*, *16*(6), 333. https://doi.org/10.3390/d16060333

Taura, L., & Gudžinskas, Z. (2025). Effect of Simulated Autogamy and Allogamy on the Success of Cephalanthera longifolia and Cephalanthera rubra (Orchidaceae) Fruit Set. *Diversity*, *17*(1), 73. https://doi.org/10.3390/d17010073

Thompson, R. M., Brose, U., Dunne, J. A., Hall, R. O., Hladyz, S., Kitching, R. L., Martinez, N. D., Rantala, H., Romanuk, T. N., Stouffer, D. B., & Tylianakis, J. M. (2012). Food webs: reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution*, *27*(12), 689–697. https://doi.org/10.1016/j.tree.2012.08.005

Thuiller, W., Albert, C., Araújo, M. B., Berry, P. M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G. F., Paterson, J., Schurr, F. M., Sykes, M. T., & Zimmermann, N. E. (2008). Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant*

Ecology, Evolution and Systematics, *9*(3–4), 137–152. https://doi.org/10.1016/j.ppees.2007.09.004

Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences*, *102*(23), 8245–8250. https://doi.org/10.1073/pnas.0409902102

Tremblay, R. L., Ackerman, J. D., Zimmerman, J. K., & Calvo, R. N. (2005). Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. *Biological Journal of the Linnean Society*, *84*(1), 1–54. https://doi.org/10.1111/j.1095-8312.2004.00400.x

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, *348*(6234), 571–573. https://doi.org/10.1126/science.aaa4984

Urban, M. C., Tewksbury, J. J., & Sheldon, K. S. (2012). On a collision course: Competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1735), 2072–2080. https://doi.org/10.1098/rspb.2011.2367

Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*(5), 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Wang, S., & Brose, U. (2018). Biodiversity and ecosystem functioning in food webs: the vertical diversity hypothesis. *Ecology Letters*, *21*(1), 9–20. https://doi.org/10.1111/ele.12865

Westerband, A. C., Funk, J. L., & Barton, K. E. (2021). Intraspecific trait variation in plants: A renewed focus on its role in ecological processes. *Annals of Botany*, *127*(4), 397–410. https://doi.org/10.1093/aob/mcab011

Woodward, G., & Hildrew, A. (2001). Invasion of a Stream Food Web by a New Top Predator. *Journal of Animal Ecology*, *70*(2), 273–288. https://doi.org/10.2307/2693425

Wootton, J. T. (2002). Indirect effects in complex ecosystems: Recent progress and future challenges. *Journal of Sea Research*, *48*(2), 157–172. https://doi.org/10.1016/S1385-1101(02)00149-1

8. PUBLICATIONS RELATED TO THE SUBJECT OF THE THESIS

First author:

Endrédi, A., Patonai, K., Podani, J., Libralato, S., Jordán, F. (2021). Who Is Where in Marine Food Webs? A Trait-Based Analysis of Network Positions. *Frontiers in Marine Science*, vol. 8, https://doi.org/10.3389/fmars.2021.636042 IF: 4.912, SJR Rank: D1

Endrédi, A.; Jordán, F.; Abonyi, A. (2018): Trait-based paradise - or only feeding the computer with biology? Forum. *Community Ecology,* 19(3): p319-321 IF: 0.746, SJR Rank: Q2

Endrédi, A.; Senánszky, V.; Libralato, S; Jordán, F. (2018): Food web dynamics in trophic hierarchies. *Ecological Modelling*, vol. 368, pp. 94-103. IF: 2.634, SJR Rank: Q2

Endrédi, A., Sőth, Á., Ércz, D., Deák, B., Valkó, O., & Nagy, J. G. (2023). Exploring life-history traits of an endangered plant (Vicia biennis L.) to support the conservation of marginal populations. *Nature Conservation*, 54, 121-147. IF (2023): 2.1, SJR Rank: Q2

Endrédi, A., Molnár, A., Nagy, J. Gy. (2015): A fokozottan védett kunsági bükkönyről. *A Puszta.* 2010-2014. vol. 25. pp. 59-62

Endrédi, A., Molnár, A., Nagy, J. Gy.(2012): A kunsági bükköny (*Vicia biennis* L.) ex-situ védelme. *Természetvédelmi Közlemények*. 18. pp. 150-158.

Co-author:

Gilián, L. D.; Endrédi, A.; Zsinka, B.; Neményi, A.; Nagy, J. Gy. (2019): Morphological and reproductive trait-variability of a food deceptive orchid, *Cephalanthera rubra* along different altitudes. *Applied Ecology and Environmental Research* 3, p5619-5639. IF(2019): 0.689, SJR rank: Q3