

ELEONORA BECCARI

Mapping and exploring trait
spaces across the tree of life



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LIST OF ORIGINAL PUBLICATIONS

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

- I **Beccari, E.** & Carmona, C.P. (2024). Aboveground and belowground sizes are aligned in the unified spectrum of plant form and function. *Nature Communications*, 15, 9199.
- II **Beccari, E.**, Capdevila, P., Salguero-Gómez, R. & Carmona, C.P. (2024). Worldwide diversity in mammalian life histories: Environmental realms and evolutionary adaptations. *Ecology Letters*, 27, e14445.
- III **Beccari, E.**, Pérez Carmona, C., Tordoni, E., Petruzzellis, F., Martinucci, D., Casagrande, G., Pavanetto, N., Rocchini, D., D'Antraccoli, M., Ciccarelli, D. & Bacaro, G. (2024). Plant spectral diversity from high-resolution multispectral imagery detects functional diversity patterns in coastal dune communities. *Journal of Vegetation Science*, 35(2), e13239.

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Author's contribution to the publications: * denotes a moderate contribution; ** denotes a large contribution; *** denotes a leading role.

	Idea development	Collecting data	Analysing data	Manuscript writing
I	**	***	***	***
II	***	***	***	***
III	**	***	***	***

LIST OF ABBREVIATIONS

Bm	=	adult body mass
D	=	fine-root diameter
Dr	=	maximum rooting depth
END	=	effective number of dimensions
Fmat	=	age at female maturity
Gest	=	gestation length
GSPFF	=	global spectrum of plant form and function
La	=	leaf area
Ln	=	leaf nitrogen concentration
Long	=	longevity
Lr	=	maximum lateral root spread
Ls	=	litter size
Ly	=	litter per year
PCA	=	principal component analysis
Ph	=	plant height
PPCA	=	phylogenetically informed principal component analysis
RES	=	root economics space
RN	=	root nitrogen concentration
RTD	=	root tissue density
SES	=	standardized effect size
Sla	=	specific leaf area
Sm	=	seed mass
SRL	=	specific root length
Ssd	=	specific stem density
TPD	=	trait probability density
UPFS	=	unified plant functional space
Wea	=	weaning length

1. INTRODUCTION

All ecological fields share a common goal: understanding the relationships between organisms and their environment (Taylor, 1936; Dice, 1955). Disentangling the reciprocal effects of organismal and environmental characteristics is essential for comprehending the eco-evolutionary processes that have shaped the diversity of life we see today (Garnier et al., 2015; Laughlin, 2023). Identifying the key characteristics of organisms that define the organization and persistence of such diversity is equally crucial, particularly for managing ecosystems and ensuring human well-being in the face of ongoing global changes (Chapin III et al., 2000; Costanza et al., 2014). In recent decades, human-induced activities have impacted climate, destroyed habitats and ecosystems, and led to the extinction of species, disrupting interactions between organisms and their environment (Powers & Jetz, 2019; Díaz et al., 2019; Farooqi et al., 2022). Understanding the drivers, effects, and trajectories of these changes is key to developing strategies for managing ecosystems under increasing anthropogenic pressures (Chapin III et al., 2000; Pettorelli, 2012; Dietz et al., 2021).

Reaching this understanding first requires ecologists to condense the vast diversity of form and function into general patterns. These generalizations should allow for comparisons of how organisms interact with each other and with the environment, while formally quantifying similarities between organisms in the response and effect that species have on ecosystems (McGill et al., 2006; Dawson et al., 2021; Mouillot et al., 2021). In modern ecology, this simplification arises from a “*convenient marriage between mathematics and natural history*” (Laughlin, 2024a). On the natural side, the form, function, and behaviour of organisms provide insights into the strategies organisms use to grow, survive, and reproduce (Stearns, 1992). For example, the number and size of offspring in mammals, akin to the number and size of seeds in plants, reflect reproductive strategies of species (Stearns, 1992; Westoby et al., 2002; Moles et al., 2005; Díaz et al., 2016). Traits—morphological, physiological, structural, phenological, or behavioural characteristics measurable at the individual level—define how organisms respond to and affect their environment (Violle et al., 2007; Díaz et al., 2013; Sobral, 2021) and act as a common currency that allows for comparisons (Cadotte et al., 2011; de Bello et al., 2021; Westoby, 2024).

On the mathematical side, algebra and geometry play a crucial role in the formal synthesis and quantification of the vast diversity of measurable traits across organisms, providing the foundation for both the construction and exploration of trait spaces (de Bello et al., 2021; Laughlin, 2023, 2024a). Trait spaces serve as accessible maps of organisms’ strategies, where organisms can be positioned based on the combination of traits they possess (Díaz et al., 2016). By mapping the set of organisms defining any ecological (from individuals, through populations and communities, to biomes and realms) and/or taxonomic (*e.g.*, species, family, class) units, it is possible to compare how such units differentiate in the occupation of trait space, and thus in the combination of traits exploited by organisms defining each unit (Cornwell et al., 2006; Carmona et al., 2016; Barajas

Barbosa et al., 2023). For this reason, trait spaces define the baseline for the quantification of trait diversity and its application in biodiversity modelling and monitoring (Levine, 2016; Mammola et al., 2021; Laughlin, 2024b; Westoby, 2024). Trait spaces form the structural backbone of this thesis, which aims to create (I and II), explore (II), and apply (III) these synthetic maps to enhance the understanding and navigation of global diversity patterns in species strategies across the tree of life. In this Introduction, I will define the concept of trait spaces (chapter 1.1) and discuss their use in quantifying organismal diversity (1.2). Next, I will review the development of global plant (1.3) and mammalian (1.4) trait spaces and their role in synthesizing species strategies. Finally, I will highlight how trait spaces may serve as powerful tools for biodiversity monitoring (1.5).

1.1. Synthesising organisms' strategies

Addressing individual traits is fundamental for understanding specific aspects of organisms' adaptations (Cadotte et al., 2011; Levine, 2016; de Bello et al., 2021). For example, traits like leaf water potential at turgor loss are key for addressing drought tolerance across communities (Bartlett et al., 2012; Petruzzellis et al., 2021) and predicting community reorganization under climate change (Tordoni et al., 2022). However, only by considering the full range of organisms' traits can we fully grasp their strategies for growth, survival, and reproduction (Stearns, 1992; Grime & Pierce, 2012; Díaz et al., 2016). Accordingly, the vast array of measurable traits in plants (Pérez-Harguindeguy et al., 2013; Kattge et al., 2020; Freschet et al., 2021; Guerrero-Ramírez et al., 2021) and animals (Myhrvold et al., 2015; Moretti et al., 2017; Tobias et al., 2022) must be summarized into few essential strategies pervasive across organisms (Laughlin, 2014, 2023; Healy et al., 2019; Mouillot et al., 2021).

For that, ecologists trying to describe organisms strategies have capitalized on the intrinsic correlations present among traits (Laughlin, 2014; Mouillot et al., 2021). For instance, plants investing in seed survival produce larger seeds with higher nutrient content and longer dormancy potential, but at the cost of reduced seed number (Westoby et al., 2002; Moles et al., 2005). Similarly, mammals with strategies prioritizing offspring survival have longer gestation and weaning periods, but fewer offspring (Grime & Pierce 2012; Stearns 1992). Given the limits that physics impose on the physiology of organisms as well as on energy use and availability, trade-offs (*i.e.*, allocation compromises) favouring investments in one trait at the expense of another are inescapable across the tree of life (Stearns, 1992; Salguero-Gómez et al., 2016; Healy et al., 2019; Brown et al., 2022). Such trade-offs constrain the range of possible strategies, defining shared investments among organisms (Díaz et al., 2016; Salguero-Gómez et al., 2016; Healy et al., 2019). Similarly, energetic balances may produce coordination among traits, which may provide redundant information in the definition of organisms' strategies (Laughlin, 2014; Mouillot et al., 2021). For instance, species that mature later in life generally allocate energy to enhancing the survival of their

young rather than in immediately producing offspring. These investments may increase long-term survival, producing longer lifespans, and thus defining a co-ordination among species' longevity and age at maturity (Stearns, 1992). Together, the structure of these correlations can reveal few fundamental dimensions of trait variation summarizing the main ecological strategies of organisms (Laughlin, 2014; Walker et al., 2017; Mouillot et al., 2021). Each dimension forms a continuum in which we can place organisms according to their trait values, so that organisms with similar traits will be positioned alongside each other (Laughlin, 2014, 2023). The combination of these fundamental synthetic dimensions defines organismal trait space (Fig. 1).

1.2. Quantifying organisms' strategies

While trait spaces allow the synthesis and visualization of organismal strategies, they also have intrinsic characteristics that make them particularly suitable for studying ecological and evolutionary questions (de Bello et al., 2021; Laughlin, 2023). On one hand, the dimensionality of a trait space, defined as the “*minimum number of independent axes needed to adequately portray trait variation of organisms*” (Laughlin, 2014), provides insights into the diversity of strategies that can be shared by the organisms under consideration. Although each dimension is a continuum that can theoretically host an infinite number of points (*i.e.*, organisms), its ecological significance is typically framed by two broad categorical strategies at its endpoints (Laughlin, 2023). For example, the trade-off between offspring number and gestation length in mammals can be represented along a single continuous dimension with two endpoint strategies (Gaillard et al., 1989; Bielby et al., 2007): investing in the quality of offspring (*i.e.*, longer gestations and fewer offsprings) or investing in reproductive quantity (*i.e.*, shorter gestations and numerous offsprings, Fig.1). While many mammals may exhibit intermediate investment strategies along this continuum, these broad categories help visualize the opposing reproductive strategies along this dimension, making it the dimension representing mammals' reproductive investment. Thus, the number of dimensions in a trait space reflects the number of broad categorical strategies that may be used by organisms, calculated as $S = 2^d$ (*sensu* Laughlin 2023), where S is the number of available strategies and d is the number of independent dimensions (Fig. 1, Laughlin, 2014, 2024b; Mouillot et al., 2021).

On the other hand, the organization of organisms in trait space reflects which of these possible strategies are realized in nature, and how often. By examining patterns in trait space (*i.e.*, trait structure of organisms, Fig. 1), it becomes possible to measure and compare different aspects of trait diversity both among and within ecological or taxonomical units (Carmona et al., 2016; Mammola et al., 2021). The amount of space occupied by a group of organisms (*i.e.*, functional richness), defined by the boundaries of the trait structure of the organisms, quantifies the extend of trait diversity within the group and provides insight into the range of strategies present (Mason et al., 2005; Carmona et al., 2016).

Additionally, measuring how densely organisms cluster in trait space helps quantify the frequency of trait combinations within these units, revealing which combinations are most prevalent (Carmona et al., 2016). By simultaneously considering the boundaries and density of an ecological or taxonomical unit's trait structure, we can assess both trait diversity and patterns of trait combinations within the unit (Mason et al., 2005; Mouillot et al., 2011). Comparing these units in terms of both components of trait structure allows for quantifying dissimilarities in trait space occupation, taking into account both the frequencies and identities of the strategies adopted by organisms (Carmona et al., 2016; Mammola et al., 2021). Thus, analysing the trait structure in trait space provides a holistic measure of trait diversity, capturing both the distribution and diversity of traits across different ecological or taxonomical units (Carmona et al., 2016; Mammola & Cardoso, 2020; Mammola et al., 2021).

Together, these intrinsic characteristics have established trait spaces as fundamental tools in trait-based approaches (Mammola et al., 2021; Westoby, 2024), applicable across spatial scales (*i.e.*, from global to local, Mouillot et al., 2011; Gaüzère et al., 2023; Tordoni et al., 2024) and levels of ecological organization (*i.e.*, from individuals to species to communities, Díaz et al., 2016; Puglielli et al., 2024). In this thesis, I will apply trait space to both plant **(I and III)** and mammals **(II)**. First, I will identify which strategies are available for global plants by exploring the dimensionality of their global trait space **(I)**. Next, I will analyse the trait structure of different mammal assemblages to investigate the ecological and evolutionary factors driving the realized diversity of mammals worldwide **(II)**. Finally, I will apply trait spaces to biodiversity monitoring, by testing whether addressing spectral diversity patterns (*i.e.*, diversity patterns of spectral band values of a remotely sensed image) can serve as a reliable tool to approximate patterns in trait diversity on the field **(III)**.

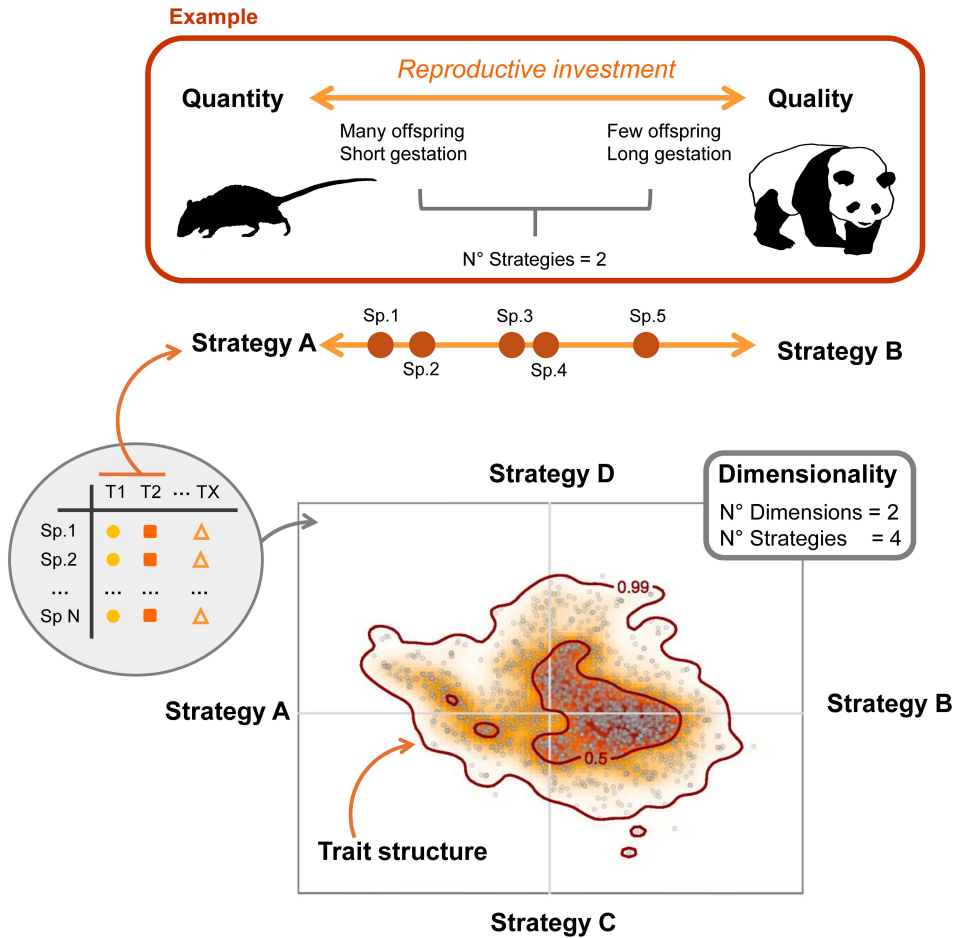


Fig. 1 Conceptual illustration of dimensionality and trait structure within a trait space. The top panel depicts the example discussed in the main text, featuring a single dimension representing mammalian reproductive investment. In this example, species vary along a continuum between investing in offspring quantity (*i.e.*, many offspring with short gestation) and offspring quality (*i.e.*, few offspring with long gestation). This single dimension captures the trade-off between offspring number and gestation length, enabling comparisons of species based on the combination of these traits and defining two opposing strategies at its endpoints. Covariation and trade-offs within a set of traits—which determine how species allocate resources to growth, reproduction, and survival (illustrated in the figure as a trait dataset for N species)—define the number of independent dimensions required to represent species' investments. These dimensions collectively define the trait space of the set of species, with their number determining the dimensionality of the trait space and, consequently, the number of broad strategies available. The pattern of species distribution within this trait space reflects the trait structure of the set of species considered. Silhouettes were downloaded from <http://www.phylopic.org>.

1.3. The dimensionality of global plant traits

The potential of trait spaces to identify common strategies shared among organisms finds one of its most promising applications in synthesizing species' trait investments on a global scale (Díaz et al., 2016; Cooke et al., 2019; Pigot et al., 2020; Bergmann et al., 2020; Cox et al., 2021). By producing maps of global species strategies, researchers can determine which trait combinations are prevalent and frequently shared across species worldwide (Laughlin, 2014; Mouillot et al., 2021; Junker et al., 2022), establishing critical baselines for applying these insights to disentangle the eco-evolutionary processes shaping current diversity patterns (Bruehlheide et al., 2018; Pigot et al., 2020; Joswig et al., 2022).

Thanks to the compilation of global trait datasets (e.g. TRY, 2019; Guerrero-Ramírez et al., 2021), plant ecologists have effectively applied trait spaces to map the global diversity of plants (Joswig et al., 2022; Tordoni et al., 2024; Li & Prentice, 2024). The seminal work by Díaz *et al.* (2016) demonstrated that the covariation of six fundamental traits related to resource use, acquisition, and reproduction can be captured by two primary dimensions, forming a plane that identifies the global spectrum of plant form and function (GSPFF, Fig. 2). The first dimension relates to plant size, while the second represents the leaf economics spectrum (Wright et al., 2004), which captures the trade-offs between resource acquisition and conservation in leaves (Díaz et al., 2016; Weigelt et al., 2021; Carmona, Bueno, et al., 2021). Within this space, species cluster in two hotspots corresponding to herbaceous species and woody species (mostly angiosperms), suggesting that only a relatively small set of trait combinations is highly frequent on a global scale (Fig. 2a).

The significance of the GSPFF lies not only in its findings but also in its potential applications. Reducing six traits to a two-dimensional plane simplifies their use in modelling frameworks, facilitating the study of relationships between traits and environmental factors (Bruehlheide et al., 2018; Joswig et al., 2022; Tordoni et al., 2024), as well as helping to disentangle the consequences of global changes, such as species extinction (Carmona, Tamme, et al., 2021). However, the GSPFF focuses solely on a subset of aboveground traits, excluding root traits, which play a fundamental role in resource uptake, storage, transport, and anchorage, thus overlooking crucial aspects of plant biology (Freschet et al., 2021; Laughlin, 2023, 2024b). Furthermore, it is important to emphasize that these findings apply to global diversity, but diversity patterns can vary significantly at finer scales (Barajas Barbosa et al., 2023).

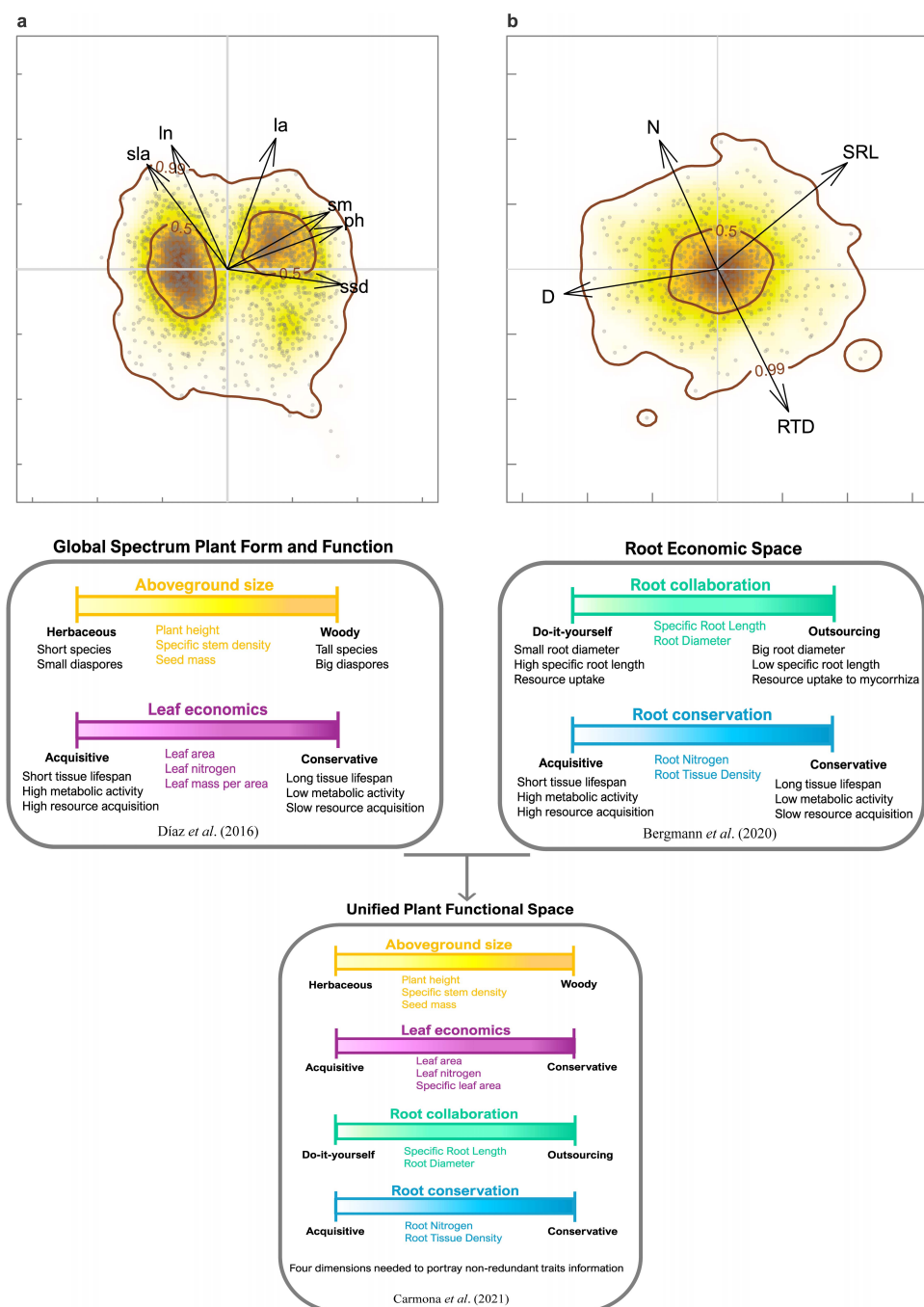


Fig. 2 Conceptual representation of the unified plant functional space (UPFS). The global spectrum of plant form and function (GSPFF) demonstrated that aboveground plant strategies can be summarised by two independent dimensions of trait variation related to plant aboveground size and to leaf economics (Díaz *et al.*, 2016). The root economics space (RES) showed that belowground plant strategies can be summarised along two main dimensions of belowground traits variation identified by the root conservation and

root collaboration gradients (Bergmann et al., 2020). A recent effort simultaneously addressing above- and belowground trait spaces (*i.e.*, unified plant functional space, UPFS; Carmona, Bueno, et al., 2021) showed a decoupling of above and belowground strategies, demonstrating that four dimensions are needed to summarise plants' investments and that these dimensions corresponded to the ones defining GSPFF and RES. Probabilistic species distribution in GSPFF and RES trait spaces are shown in panel **a** and **b**, respectively. The colour gradient depicts different densities of species in the space (the brown areas have higher density of species). The arrow lengths are proportional to the loadings of the traits considered in defining the dimensions of the two spaces. The aboveground traits are specific leaf area (sla), leaf nitrogen concentration (ln), leaf area (la), seed mass (sm), plant height (ph), and specific stem density (ssd). The fine root traits are specific root length (SRL), root diameter (D), root tissue density (RTD) and root nitrogen concentration (N). The thick contour lines indicate the probability densities at 0.5 and 0.99 quantiles of the probabilistic distribution of species in the trait space. In this figure both GSPFF and RES spaces were built using the same set of data of paper I and the same TPD framework used in paper II.

The recent compilation of global fine root datasets (Iversen et al., 2017; Guerrero-Ramírez et al., 2021; Iversen & McCormack, 2021) enabled the creation of a similar framework tackling some of the belowground components of plant strategies. The root economics space (RES; Bergmann *et al.* 2020) reveals the bi-dimensionality of fine root investments (Fig. 2). The first axis defines the collaboration gradient, which portrays the trade-off between species with finer roots suited for independent resource acquisition, and species with thicker roots that rely on mycorrhizal partnerships. The second dimension reflects a continuum similar to the leaf economics spectrum, known as the conservation gradient, with conservative species investing in high root tissue density and acquisitive species constructing more metabolically active tissue, showing higher nitrogen content (Fig. 2).

Subsequent efforts integrated above- and belowground traits into a single framework (Weigelt et al., 2021; Carmona, Bueno, et al., 2021), here defined the unified plant functional space (UPFS, Fig. 2). Carmona *et al.* (2021a) combined the traits from the GSPFF and RES, demonstrating that four dimensions are needed to portray global plant strategies, as aboveground and fine-root investments are largely independent. This independence is further stressed by the decoupled organization of species in the planes (Fig. 2ab, Carmona, Bueno, et al., 2021). In contrast, Weigelt *et al.* (2021) proposed a potential coordination between the leaf economics spectrum and the conservation dimension of the RES, with a fourth dimension defined by species' rooting depth (see also Weigelt *et al.* 2023). However, Bueno *et al.* (2023) supported the integrity of the UPFS, suggesting that the divergent conclusions between the two studies arise from different interpretations of trait alignment in otherwise equivalent spaces.

While these studies provide crucial insights into plant strategy diversity, they also highlight a key issue: we are still far from reaching a unified consensus on a global UPFS. To accurately portray global diversity in plant strategies, it is essential to include underrepresented yet fundamental traits—such as clonality (Klimešová et al., 2021) or drought resistance (Laughlin et al., 2023)—as well as

species from diverse regions, particularly tropical and subtropical zones (Maitner et al., 2023). Including additional observations could significantly alter the correlation structure within a trait space, potentially redefining the relationships that shape its dimensions and, by extension, their ecological meaning (Laughlin, 2014, 2023). Moreover, the inclusion of traits not correlated with the current dimensions would likely increase the dimensionality of the space. Likewise, adding neglected species with previously overlooked adaptations could similarly expand trait space. This suggests that incorporating new data into trait space analysis could uncover overlooked strategies available in nature (Laughlin, 2014, 2023).

One unresolved aspect of plant function is how root size fits within the UPFS. Weigelt et al., (2021) proposed that rooting depth in the UPFS should support the hypothesis that above- and belowground sizes are not always coordinated: while tall plants require water and nutrients to meet their transpiration and photosynthetic demands, having deep roots does not necessarily enhance resource acquisition. Contrastingly, a more recent study using a broader dataset revealed a strong positive correlation between above- and belowground size traits (Tumber-Dávila et al., 2022). This finding aligns with allometric scaling predictions, which suggest strong relationships in biomass distribution across plant organs (Niklas & Enquist, 2001; Enquist & Niklas, 2002; Smith-Martin et al., 2020). These results suggest that incorporating root size traits into the UPFS framework may not increase its dimensionality. The contrast between these findings highlights that the issue of size coordination between above- and belowground components remains unresolved, complicating our understanding of how resource allocation to growth influences the UPFS. It also underscores the importance of continuously updating global trait spaces, such as the UPFS, as new significant data and observations emerge. This is crucial to avoid biased interpretations and misleading results in their application.

1.4. A global trait space for mammals

While global synthesis of plant traits have advanced significantly, an equivalent comprehensive framework for animals has yet to emerge (Junker et al., 2022; Schleuning et al., 2023). The success of trait-based approaches in disentangling biodiversity has driven a recent growth in the compilation of animal trait datasets (Junker et al., 2022; Schleuning et al., 2023), which are promising but still highly incomplete (Myhrvold et al., 2015; Soria et al., 2021; Herberstein et al., 2022). Notably, there is a stark contrast in the difficulty of measuring plant and animal traits. For instance, measuring leaf area in plants is relatively simple compared to tracking the gestation length of a marine mammal like a seal. However, this increasing compilation of trait databases, along with trait imputation methods (Penone et al., 2014; Stewart et al., 2023; Moura et al., 2024), has led to a recent explosion in the application of trait spaces to animal ecology (*e.g.* Pigot et al., 2020; Carmona, Tamme, et al., 2021; Toussaint et al., 2021; Rodríguez-Caro et

al., 2023). Yet, global efforts comparable to the UPFS of plants, are still lacking (Junker et al., 2022).

Mammals are an ideal starting point for such efforts. Indeed, primary studies covering a few hundred of mostly terrestrial species have already identified key dimensions of traits variation (Gaillard et al., 1989; Bielby et al., 2007). The first dimension generally reflects the fast–slow continuum, representing the time scale of life, while the second pertains to the timing and intensity of reproduction (Gaillard et al., 1989; Bielby et al., 2007; Capdevila et al., 2020) and is more dependent on the subset of species considered. These efforts have highlighted the set of life history traits fundamental for starting the construction of a global mammalian trait space, paving the way for its further expansion (Gaillard et al., 1989; Bielby et al., 2007). However, without including the full set of mammalian adaptations and without addressing their organization in the trait space, the tool remains incomplete.

Similar to what was discussed for plants, the inclusion of species from under-represented environments or with unrepresented adaptations may modify the ecological interpretation of the axes built on a few hundred species (see for exact species number Gaillard et al., 1989; Bielby et al., 2007), thereby revealing previously overlooked strategies. Likewise, directional selection driven by different environments and mode of life (*e.g.* arboreality, fossoriality, Healy et al., 2014) may result in shared trait combinations at the global scale, which may lead to clustering patterns in mammalian trait space (Carmona, Tamme, et al., 2021; Cox et al., 2021). Mammals are ubiquitous, ranging across diverse realms and habitats—from land (Burgin et al., 2018; Grossnickle et al., 2019), trees (Shattuck & Williams, 2010), and burrows (Healy et al., 2014), to air (Babich Morrow et al., 2021), and varying degrees of aquatic relation (*i.e.* aquatic and semi-aquatic, Davis, 2019). The distinct environmental pressures experienced across these habitats are known to select for different combinations of life history traits (Stearns, 1992). For instance, the ability to climb trees or fly is generally associated with longer lifespans (Healy et al., 2014; Babich Morrow et al., 2021), while aquatic species typically produce single offspring (Davis, 2019). As a result, different strategies are favoured in different environments, leading to environment-driven clustering in trait space. However, without a global synthesis mapping mammalian trait variation, questions about the diversity and prevalence of mammalian strategies remain unresolved, hindering their application in disentangling diversity patterns in relation to the environment and its changes.

1.5. Trait spaces in diversity monitoring

If global trait spaces provide a baseline for exploring evolutionary and biogeographical drivers of species strategies, their application in comparing communities helps disentangle finer ecological mechanisms (*e.g.*, niche differentiation, competition) that drive trait diversity (Díaz & Cabido, 2001; Lamanna et al., 2014; Jarzyna & Jetz, 2018). By using trait spaces to measure community diversity across both space (Lamanna et al., 2014) and time (Trindade et al., 2023), it is possible to gain insights into how ecosystems function, respond to environmental changes, maintain biodiversity (Mason et al., 2005; Díaz et al., 2007), and will rearrange over time (Andrew et al., 2022; Tordoni et al., 2023; Wu et al., 2023).

However, to keep pace with the rapid impacts of global change on ecosystems (Díaz et al., 2019; Trisos et al., 2020), it is crucial to monitor and measure biodiversity in a fast, repeatable, and spatially extensive manner. Remote sensing offers a promising solution to this challenge (Jetz et al., 2016; Yannelli et al., 2022). It leverages the fact that variations in plant morphology, physiology, and chemical characteristics result in phenotypic differences (Wang & Gamon, 2019; Fassnacht et al., 2022), which are captured as distinct spectral band values in remotely sensed images (Palmer et al., 2002; Rocchini et al., 2004). Therefore, examining the diversity of spectral bands (*i.e.*, spectral diversity) across space and time can serve as a proxy for different aspects of vegetation diversity, including taxonomic and trait diversity (Gholizadeh et al., 2019; Wang & Gamon, 2019; Gamon et al., 2020; Frye et al., 2021).

While many studies have tested the effectiveness of remote sensing in approximating trait measurements and diversity (Ali et al., 2017; Durán et al., 2019; Aguirre-Gutiérrez et al., 2021), they often focus on single aspects of trait variation (*e.g.*, Rocchini et al., 2017; Gholizadeh et al., 2019; Torresani et al., 2019), overlooking patterns of trait diversity within and between plant communities (Laliberté et al., 2020). Addressing only specific components, like means (community-weighted mean; Ricotta & Moretti, 2011), variance (Rao's Q; de Bello et al., 2016), or the amount of trait space occupied by species (convex hull; Villéger et al., 2008), provides a limited view of trait diversity, especially when compared to the holistic insights obtained from analysing trait structures (Mason et al., 2005; Carmona et al., 2016; Mammola et al., 2021). However, the concept of retrieving diversity and frequency patterns from the structure of points in a synthetic space is not exclusive to trait-based frameworks (Blonder, 2018; Mammola et al., 2021). Any set of two or more continuous variables can define a space from which extension and clustering patterns can be extracted and, eventually, related to trait measurements (*e.g.*, climate or stress tolerance spaces; Vásquez-Valderrama et al., 2022; Pavanetto et al., 2024). This idea may hold the key to linking spectral and trait diversity by accounting for all multivariate components. Since the spectral features of plants are driven by their phenotypes, mapping pixel positions in a spectral space (*i.e.*, defined by spectral band values

of the pixels) could enable the mapping of trait combinations underlying those phenotypes. In theory, the organization of pixels in a spectral space should reflect the organization of species in a trait space, with the most frequent pixel combinations corresponding to the most prevalent trait combinations observed on the ground. By extracting spectral structures (*i.e.*, patterns of organization of pixels in a spectral space), it may be possible to approximate the trait structure of plant communities, considering both range and frequency of prevalent trait combinations. This approach, using imagery from drones or satellites, could provide a holistic, repeatable, and fast way to assess trait diversity over large areas. However, the ability of the spectral space to reliably approximate trait space patterns across communities remains largely unexplored and theoretical. As a result, it is difficult to fully assess the potential of remote sensing for rapidly approximating plant trait patterns and monitoring changes over time.

1.6. Aims of the thesis

The primary objective of this thesis is to fill the gaps in the creation and application of trait spaces to map trait diversity across different species groups. Specifically, this thesis aims to:

1. Expand the UPFS by testing whether the inclusion of the most up-to-date dataset on root size traits (*i.e.*, maximum lateral root spread and maximum rooting depth) affects the number and identity of dimensions summarizing global plant strategies (**I**). Strong correlations observed between above- and belowground size traits suggest that plant size investment may align along a single axis, without increasing the dimensionality or the number of strategies available for global plants.
2. Create a unified mammalian trait space that encompasses all global adaptations, ranging from polar to desert environments and from aerial to aquatic life. This space will be used to examine the influence of environmental realms (air, water, land) and modes of life in shaping diversity patterns in mammalian life history strategies (**II**). Given that both environment and mode of life appear to select for specific trait combinations, species are expected to cluster within life history space depending on whether they inhabit similar environmental realms or have similar modes of life.
3. Integrate trait spaces into remote sensing frameworks to derive patterns of spectral diversity and examine their relationship with trait diversity patterns in plant communities across an environmental gradient (**III**). Given the observed relationship between functional and spectral diversity, the organization of pixels in spectral space is expected to mirror trait space patterns, serving as an effective proxy for monitoring trait diversity.

2. METHODS

2.1. Aggregating global datasets

To construct trait spaces that represent global species, it is crucial to rely on published datasets that are carefully aggregated (**I**, **II**). These datasets are often incomplete, with the degree of missingness varying across taxa and traits (Stewart et al., 2023). Since trait spaces can be built using dimensionality reduction techniques applied to a trait correlation matrix (Legendre & Legendre, 2012)—which can be computed independently of missing traits—data incompleteness does not hinder the identification of the main dimensions of trait variation (**I**). However, when examining species' occupation patterns within trait space (**II**), it is essential to project species into the space, and this can only be done for species with complete trait information (Legendre & Legendre, 2012). Trait imputation methods can fill the gaps in these global datasets, enhancing the completeness of trait information used to build the trait space and enabling the estimation of patterns in trait covariation for global species (**II**).

In paper **I**, the dataset was assembled based on the latest UPFS framework (Carmona, Bueno, et al., 2021). I downloaded the six aboveground traits that comprise the GSPFF (Fig. 2a, Díaz et al., 2016) from the TRY database (TRY, 2019) and the four fine root traits that define RES (Fig. 2b, Bergmann et al., 2020) from the GRooT dataset (Guerrero-Ramírez et al., 2021). The data were assembled using the same subset of traits and the same data processing described in Carmona, Bueno, et al., (2021), resulting in a UPFS dataset that includes ten plant traits: plant height (ph, measured in m), specific stem density (ssd, g/m^3), seed mass (sm, mg), leaf area (la, mm^2), leaf nitrogen concentration (ln, mg/g), specific leaf area (sla, mm^2/mg), specific root length (SRL, m/g), root diameter (D, mm), root tissue density (RTD, g/cm^3) and root nitrogen concentration (RN, mg/g). I combined the UPFS dataset with root size data available from Tumber-Dávila et al., (2022), which included observations on maximum rooting depth (Dr, measured in m), and maximum lateral root spread (Lr, one-sided, m). The final dataset contained 39,334 plant species and twelve traits with varying levels of completeness, with pairs of traits having common observations ranging from a minimum of 257 common species (for root nitrogen and lateral root spread) to a maximum of 7,217 (plant height and seed mass). The dataset comprised 49.47% woody species and 32.04% herbaceous species, with 18.29% of species missing woodiness information. Woodiness information was sourced from Carmona, Bueno, et al., (2021).

In paper **II**, I used the Amniote dataset (Myhrvold et al., 2015), which contains life history observations for 4,953 mammalian species worldwide. I selected only the most complete set of life history traits (*i.e.*, trait records for at least 1,000 species), resulting in a dataset with six traits: litter size (ls, number of offspring per reproductive event), litter per year (ly, number of litters per year), age at female maturity (fmat, time needed for female individuals to reach maturity in days),

weaning length (wea, time needed to wean the offspring in days), gestation length (gest, time passing between conception and birth in days), longevity (long, individual lifespan in years), and adult body mass (bm, in grams). Then, I imputed missing life history trait records. Since accounting for evolutionary relationships improves the accuracy of imputation (Penone et al., 2014), I downloaded the complete fossil-based set of 10,000 mammalian phylogenies from the Vertlife database (Upham et al., 2019), which I aggregated to create a single maximum clade credibility tree. For the imputation procedure, I selected mammalian species with information on body size and at least one of the other life history traits considered (*i.e.*, ls, ly, fmat, wea, gest, long). Then, following the procedure of Carmona, Tamme, et al., (2021), I incorporated phylogenetic information into the imputation process by using the first 10 phylogenetic eigenvectors derived from the phylogenetic tree and imputed missing trait information using random forest algorithms (Stekhoven, 2022). The accuracy of the imputation procedure was checked following Carmona, Tamme, et al., (2021).

To test whether differences in environmental realms and modes of life influence patterns in mammalian life history diversity, I classified mammalian species as aquatic, semi-aquatic, aerial, and terrestrial based on the WoRMS (WoRMS Editorial Board, 2020) and IUCN (IUCN, 2017) datasets. I created an Aquatic Dependency Index (AD Index) to refine the labelling of unresolved aquatic, terrestrial, and semi-aquatic classifications. The AD Index is based on the responses to a series of binary questions related to the amount of time spent in water during fundamental phases of species' life histories (*e.g.*, birth, mating). Species scoring zero in the AD Index (*i.e.*, no important parts of life are strictly constrained by water presence) were classified as terrestrial, species scoring 5 out of a maximum of 5 (*i.e.*, species that spend their whole life in water) were classified as aquatic, while species with intermediate scores were classified as semi-aquatic. Terrestrial species were further classified according to their mode of life into arboreal, semi-arboreal, and fossorial mode of life following Santini et al., (2022). The procedure resulted in a final dataset of 3,438 mammalian species (53.7% of currently recognised living mammals, Burgin et al., 2018) from 29 orders.

2.2. Study area and remote sensing data

Paper **III** was the only one relying on on-field measurements. Fieldwork was performed in May–June 2019 along a protected coastal sand dune habitat in Tuscany (Italy). Given the aim of testing the effectiveness of a remote approximation of trait diversity patterns along an environmental gradient, the coastal dune ecosystem was an ideal choice. On one hand, coastal dunes are characterized by steep ecological gradients (Tordoni et al., 2021), which result in distinct vegetation zonation arranged from the sea to inland (Acosta et al., 2007). On the other hand, coastal dunes feature patchy vegetation dominated by herbaceous species and a

single woody species (*Juniperus* spp.), allowing for clear retrieval of vegetation images without canopy layering obscuring understory species. Sampling was based on a square grid of 500×500 m overlaying the whole study area, with six transects spanning from sea to inland selected, one for each cell of the grid. Transect length ranged between 172 and 208 m, depending on dune morphology, and encompassed a set of contiguous square plots of 16 m² each, for a total of 288 plots across the six transects. In each plot, occurrences and abundance of vascular plant species (measured as percentage visual cover) were assessed.

Leaf samples for trait measurements were randomly collected across all transects. We sampled 2–4 individuals for each species at the extremes of the environmental gradient (*i.e.*, foredune and fixed dune). In total, functional traits were measured on 42 out of 75 recorded species, accounting for 97.4% of the total plant coverage. We measured traits associated with leaf economics (leaf economics spectrum, Wright et al., 2004, Fig. 2) and both water safety and water use efficiency (Sack et al., 2013): specific leaf area (SLA, mm²/mg); leaf dry matter content (LDMC, mg/g); minor vein length per unit area (VLA_{minor}, mm/mm²); water potential at turgor loss point (Ψ_{tlp} , MPa). Traits were measured following the same procedure as in Petruzzellis et al., (2021). Trait measurements were then averaged at the species level.

Remotely sensed image acquisition was performed immediately before vegetation sampling. We conducted an Unmanned Aerial Vehicle survey using a multispectral camera capturing five multispectral bands: blue (centre wavelength: 475 nm), green (560 nm), red (668 nm), near infrared (NIR, 840 nm), and red edge (RE, 717 nm). We acquired one image per transect at a pixel resolution of 3 cm that was processed to remove all pixels not related to vegetation through an unsupervised linear spectral unmixing process (Settle & Drake, 1993). The sand-cleaning procedure produced a total of ca. 1.5 million pixels used for subsequent analysis.

2.3. Building trait spaces

The orthogonality of trait dimensions is fundamental for the accurate discrimination of species in a trait space (Laughlin, 2014). Accordingly, principal component analysis (PCA) and its underlying mathematical process (*i.e.*, eigendecomposition, Legendre & Legendre, 2012) were used for the construction of trait (**I**, **II**, **III**) and spectral (**III**) spaces across all works in the thesis. However, different data correction and trait subsets were used in each study.

In paper **I**, to test whether the inclusion of root size traits affects the dimensionality and trait structure observed in the original UPFS, I performed a series of four eigendecompositions, progressively including root size traits into the set of ten traits used to represent the original UPFS (Carmona, Bueno, et al., 2021):

- 1) UPFS traits (above- and belowground traits),
- 2) UPFS traits and rooting depth (Dr),

- 3) UPFS traits and lateral root spread (Lr),
- 4) UPFS and root size traits (above- and belowground traits with both root size traits).

Each eigendecomposition was based on a trait correlation matrix calculated using Pearson correlation coefficients. Eigendecomposing a matrix of trait correlations is equivalent to performing PCA on trait correlations. However, it allows the inclusion of all species with mutual information for each pair of traits, rather than following the commonly used PCA procedure, which discards species missing any trait and thereby represents a non-random subset of species (Sandel et al., 2015).

Given the strong allometric constraints that affect life history trait covariation (Bielby et al., 2007; Sibly & Brown, 2007; Jeschke & Kokko, 2009), in paper II, I first accounted for the effect of body mass before computing the mammalian life history space. To do this, I performed a series of ordinary linear regressions between individual life history traits and species' adult body mass. I then extracted body mass-corrected residuals for each species from each regression, which were used as the six size-corrected life history traits for constructing the trait spaces through a PCA. As a result, a single trait space was produced, considering all 3,438 mammalian species, and used across all analyses.

In paper III, trait and spectral spaces were constructed using the full set of trait and band values available by performing a PCA on species and pixel data, respectively. Accordingly, all analyses were based on a single trait space that included all 42 species and a single spectral space that included approximately 1.5 million pixels.

2.4. Dimensionality and trait correlation structure in a trait space

For each space, I determined the number of relevant dimensions needed to capture non-redundant trait variation by retaining dimensions with eigenvalues > 1 (*i.e.*, Kaiser Rule, Legendre & Legendre, 2012; I, II) or by using Horn's parallel analysis (Dinno, 2018; III). I refer to trait spaces that include only the relevant dimensions as '*reduced spaces*', while those that include all dimensions are simply called '*spaces*'.

Trait loadings represent the correlations between traits and the dimensions of a space, identifying the variables that contribute most to each dimension (Legendre & Legendre, 2012) and providing ecological interpretation. This ecological interpretation of trait space dimensions often relies solely on bidimensional projections of these loadings. However, for global syntheses aimed at uncovering universally shared trait relationships, especially when the reduced space is multidimensional (I, II), interpreting trait relationships based solely on bivariate

projections of dimension loadings risks overlooking information contained in other dimensions. This approach may lead to biased estimates of the trait relationships defining the reduced space, thereby affecting the identification of the broad categorical strategies available for global species (Carmona, Bueno, et al., 2021; Bueno et al., 2023). To avoid this bias, in both paper **I** and **II**, I extracted the angles between traits in the reduced global spaces, following the procedure described by Bueno et al., (2023). These angles offer a comprehensive understanding of trait relationships, as they represent the precise correspondence of multidimensional correlations across all dimensions of the reduced space, with the multidimensional correlation expressed as the cosine of the trait angle. A trait angle of 90° indicates no correlation between traits, while angles of 0° and 180° indicate perfect positive and negative correlations, respectively. In paper **I**, to test the effect of including root size traits on the correlation structure shaping global plant trait spaces, I calculated the Pearson correlation coefficient (r) between the angles in the reduced space constructed with UPFS and those in reduced spaces progressively incorporating root size traits.

In paper **I**, the aim of testing whether the inclusion of root size traits alters UPFS involves not only determining whether adding root size traits changes the trait relationships, but also whether it affects the number of dimensions needed to capture trait variation. To compare trait spaces with different trait subsets, and thus different levels of variation, a more refined estimation than simply counting relevant dimensions is needed. For that, I expanded the equivalent species framework proposed by Jost (2006, 2007) by calculating the effective number of dimensions (END) as the inverse of Simpson's diversity index, using the eigenvalues of each space. As inverse Simpson, END provides a standardized measure of the number of dimensions explaining the same variance needed to capture trait variation in the dataset. It ranges from perfect covariation ($END = 1$) to no correlation among traits ($END = \text{the number of traits used to build the trait space}$). Then, I created a null model to compare the increase in END observed after adding root size traits with the change in dimensionality expected if an uncorrelated trait were added to the UPFS. To do this, I simulated a random uncorrelated trait by sampling from a normal distribution with a mean of 0 and a standard deviation of 1. I added this simulated trait to the subset of traits defining the UPFS (excluding root size traits), performed an eigendecomposition, and estimated the END of the resulting space. I repeated this procedure 500 times to obtain a null distribution of END. Finally, I used the mean END of the simulated space as a reference to assess the extent to which including root size traits approximates adding an uncorrelated trait to the UPFS.

2.5. Extracting patterns in space occupation: trait structures of species

The trait structure of species in reduced spaces (*i.e.*, patterns of species organization), considering both the extent of the boundaries and the density of species, can be extracted using probabilistic hypervolume approaches (Carmona et al., 2016; Blonder, 2018; Mammola et al., 2021). For this purpose, I used the trait probability density (TPD; Carmona et al., 2016) framework (**II**, **III**), which estimates trait structure as probability density functions that reflect the probabilistic distribution of species (or pixels) in a (reduced) space.

TPD functions can be used to quantify different aspects of trait variation, like functional richness (*i.e.*, the amount of space occupied by species, Mason et al., 2005) or functional divergence (*i.e.*, the degree to which species' density is skewed towards the extremes of the occupied space, Mason et al., 2005). They can also be used to extract dissimilarities among ecological units in the space (Carmona et al., 2016). Specifically, the TPD framework calculates dissimilarities among trait structures as 1-overlap of the considered TPD functions, producing measures varying between 1 (indicating a complete overlap between the considered functions) and 0 (when the two functions are completely disjoint). Overlap-based dissimilarities consider both differences in the boundaries and differences in the density of occupation of the space and can be further decomposed into two complementary components: one quantifying up to what point differences between trait structures are related to the occupation of exclusive regions of the space (turnover) and another reflecting how differently species occupy the shared parts of the reduced space (nestedness; Carmona et al., 2016; Carmona, 2019).

To explore diversity and patterns in life history trait combinations of global mammals (**II**), I extracted the trait structure of the entire set of mammal species by weighting all species' kernels and aggregating them to form a single continuous TPD function across the whole mammalian life history space. The value of the TPD function at any given point in the life history space reflects the density of species in that specific area of the space (Carmona et al., 2016; Carmona, 2019). Then, I created single TPD functions for each environmental realm and mode of life by aggregating the species characteristic of each realm or mode of life' category. For each TPD function, I calculated functional richness and divergence, and computed overlap-based dissimilarity among all pairwise categories of environmental realms and modes of life.

Similarly, in paper **III**, I derived trait and spectral structures for each plot using the TPD framework (Carmona et al., 2016; Carmona, 2019). I used plot structure to extract different aspects of trait and spectral diversity across the different hierarchical scales of the study. Specifically, I extracted functional (and spectral) richness to measure diversity present within plots (α -diversity). Then, I measured the overlap-based dissimilarities between pairs of plots from the same transect, to address differences in extent and patterns of trait (spectral) diversity within each transect (β -diversity). Finally, I estimated γ -diversity by deriving a single trait and spectral structure considering all species and pixels present in the spaces.

2.6. Comparing trait structures: adjusting for species richness and shared ancestry

Trait structures of species within a trait space are often closely linked to the species richness of the ecological or taxonomic units considered, especially concerning the extent of their boundaries (Mouillot et al., 2021; Carmona, Bueno, et al., 2021). Depending on the dimensionality of the trait space and the complementarity of species within a group (Petchey & Gaston, 2002; Mason et al., 2005), communities with higher species richness are generally more likely to diversify in the trait set used, leading to an increase in functional richness (Petchey & Gaston, 2002; Mason et al., 2005; Mouillot et al., 2021). Consequently, to avoid biases and enable meaningful comparisons of trait diversity across environmental realms and modes of life with varying species numbers, it is essential to use metrics unaffected by species count (**II**). For this, I constructed a null model randomly selecting the same number of species observed in each environmental realm and mode of life from the full set of mammals. This random subset was used to derive a random trait structure within the trait space, from which I calculated functional richness. I iterated this randomization 999 times for each group. I then calculated the standardized effect size (SES) as: $SES = (\text{observed value} - \text{mean of randomized values}) / \text{standard deviation of randomized values}$. Negative SES values indicate that the species in a group are more clustered within the trait space (occupying a smaller area, with high trait redundancy) than expected from a random sample of the same size, and vice versa. Finally, I used SES values of each group to test for statistically significant deviations from expected functional richness, I computed two-sided p-values by comparing each SES value to a cumulative normal distribution with a mean of 0 and standard deviation of 1.

Because overlap-based dissimilarities reflect differences in both boundaries and species density within a trait space (Carmona, Tamme, et al., 2021; Toussaint et al., 2021) and can be influenced, albeit to a lesser extent than functional richness, by variations in species numbers across mammalian groups. Accordingly, I performed an additional null model to control for these effects when comparing mammalian group dissimilarities (**II**). In this model, I included only species shared between each pair of realms or modes of life and randomized their group classifications, preserving observed species counts per group and ensuring no species were assigned to multiple groups. For each iteration of the null model ($n = 999$), I estimated a random trait structure and calculated overlap-based dissimilarity, along with its nestedness and turnover components. Finally, I computed SES values for all measures using the same formula as above.

Given that both environmental filtering and evolutionary history shape trait correlations defining a trait space (Stearns, 1992; Revell & Harmon, 2022; Westoby et al., 2023), trait convergence among species within an environmental realm or mode of life may largely result from the shared ancestry of species (de Bello et al., 2015; Westoby et al., 2023). Thus, I tested whether observed patterns held among closely related species and after accounting for species non-inde-

pendence (II). For each mammalian order, I estimated the centroid of the trait structure within each environmental realm and mode of life associated with the species in that order. These centroids were then used to test for significant differences in centroid positions across realms and mode of life using a linear mixed-effects model, where the mean score of the order along each principal component was the response variable, environmental realm or mode of life was the fixed effect, and mammalian order was a random intercept. Separate models were performed for each PC, each category of mode of life, and environmental realm. Next, to formally examine whether the relationships among species' life history strategies, environmental realms, and modes of life remained consistent irrespective of phylogenetic relatedness, I conducted a series of Phylogenetic Generalized Least Squares regressions (PGLS, Symonds & Blomberg, 2014; Revell & Harmon, 2022). Four PGLS models were applied: one for each dimension of the trait space, and one each for environmental realms and mode of life. In each model, species position was the response variable and environmental realm, or modes of life, were the predictors.

2.7. Relating diversity measures along an environmental gradient

In paper III, to test the hypothesis that patterns in trait structure can be detected remotely, I related trait and spectral measurements across different scales of the study. First, I visually compared trait and spectral structures of the entire study area and individual transects by plotting their TPD functions at various probability quantiles. Next, I assessed the correlation between trait and spectral overlap-based dissimilarities across plot pairs using Mantel tests (Legendre & Legendre, 2012), extracting the Spearman correlation coefficient (ρ). I then performed a major-axis regression for each transect to examine the relationship between trait and spectral overlap-based dissimilarities. Finally, I used major-axis regression within each transect to estimate the relationships between functional and spectral richness (Legendre & Legendre, 2012).

To test whether trait and spectral diversity patterns are coordinated along the sea—inland gradient (III), I conducted a series of models along the transects. Given the non-linear biodiversity patterns along coastal dunes (Acosta et al., 2007), I applied Generalized Additive Models (GAMs) for each transect, with overlap-based dissimilarity as the response variable and the interaction between spatial distance (*i.e.*, Euclidean distance between plots) and the type of diversity facet (*i.e.*, spectral or trait diversity) as predictors. Then, I estimated the relationships between richness values (response variable) and the interaction between distance from the sea and the type of diversity facet. To do that, I performed a separate GAM model for each transect.

All analyses (I, II, III) were performed using R (R Core Team, 2020). For detailed package and methodologies please refer to publications.

3. RESULTS

3.1. Dimensionality of global plant traits

The reduced space constructed by considering UPFS and root size traits included four relevant dimensions of main trait variation, together explaining 72.31% of the total variance (**I**). The first dimension (32.14% of total variance) reflected the positive correlations observed among above- and belowground size traits (Fig. 3). The second and third dimensions (16.18% and 14.72% of total variance, respectively) highlighted the trade-off between specific root length and root diameter as well as the covariation among traits related to the leaf economics spectrum (*i.e.*, specific leaf area and leaf nitrogen, Fig. 3). The fourth dimension (9.26% of total variance) represented the trade-off between root nitrogen and root tissue density (Fig. 3). This coordination of above- and belowground size on the first dimension of the UPFS was observed regardless of the root traits subset considered.

The inclusion of lateral root spread and maximum rooting depth did not alter the trait correlation structure shaping the UPFS (**I**). Angles between traits in the reduced space representing the same ecological dimensions in the UPFS (*i.e.*, above- and belowground size, leaf economic spectrum, root collaboration, root conservation) were consistently either close to 0 degrees (indicating positive covariation) or close to 180 degrees (indicating trade-offs). Specifically, angles between above- and belowground size traits were consistently low, ranging from 14.1° between plant height and lateral root spread ($r = 0.95$) to 25.7° between specific stem density and rooting depth ($r = 0.64$). Correlations across angles in UPFS and in UPFS progressively including root size traits were strong and positive, as indicated by Pearson's correlation coefficients among angles close to 1. This indicates that the fundamental relationships between traits in the reduced spaces are unaffected by the inclusion of root-size traits.

The inclusion of root size did not significantly increase UPFS dimensionality, confirming that root size variation is already accounted for in the UPFS (**I**). Indeed, the original UPFS (without root size traits) had 5.67 equivalent dimensions (END), and including root size traits increased END by much less than expected under the inclusion of an uncorrelated trait (Fig. 3): 2.02% increase when only lateral root spread was added, 24.40% increase when only rooting depth was added, and 12.65% increase when both root size traits were added (Fig. 3).

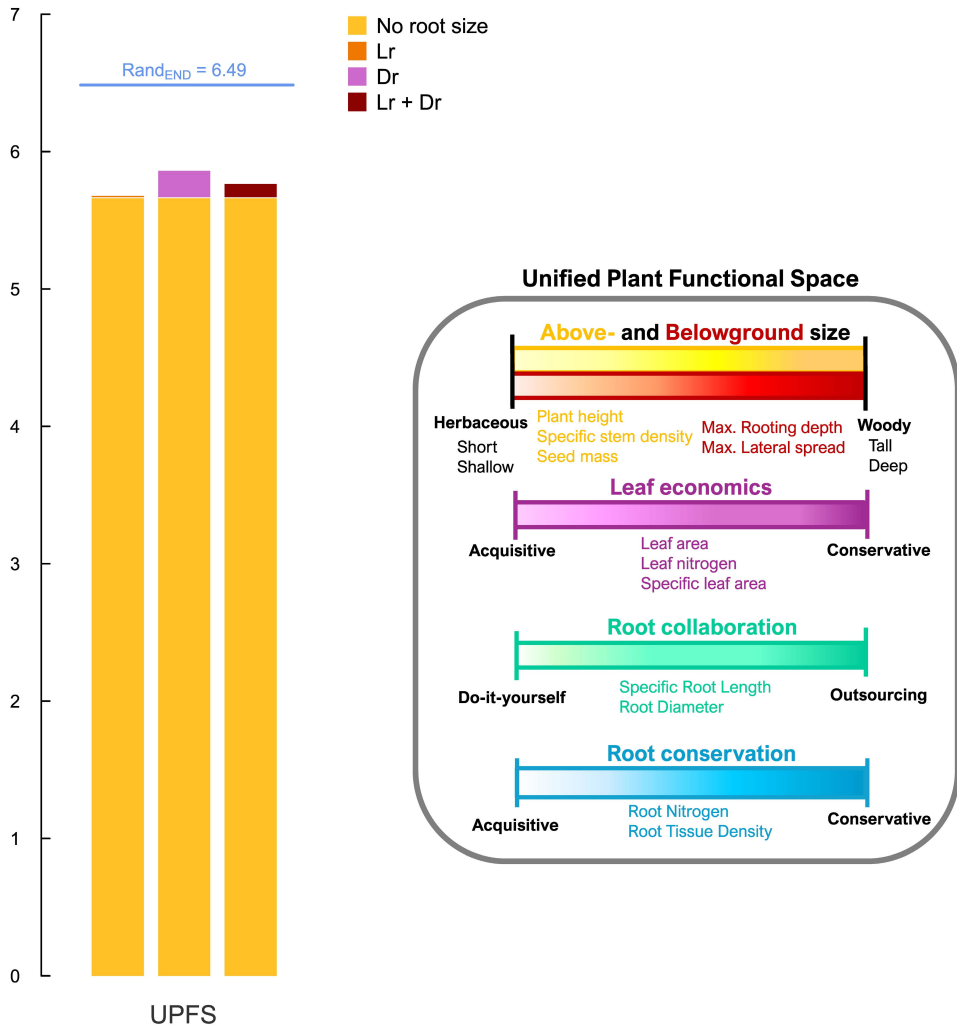


Fig. 3 Left panel: effective number of dimensions (END) across UPFS traits subsets with different levels of root size inclusion. No root size: space excluding root size traits (yellow); Lr: space considering only lateral root spread (orange); Dr: space considering only rooting depth (pink); Lr + Dr: space considering both root size traits (dark red). Blue lines represent the END expected if we add a random uncorrelated trait to UPFS ($Rand_{END}$). Right panel: conceptual representation of the effect of root size traits inclusion in the UPFS. Since, above and belowground traits are coordinated at the global scale, root size traits align along the aboveground size dimension. In the conceptual figure each line represents an independent dimension of the trait space. Traits defining each independent dimension are in the same colours of the dimension they load on. In bold black are shown the opposite broad plant categorical strategies portrayed along each dimension. Adapted from paper I Fig. 1 and Fig. 4.

3.2. Patterns in mammalian strategies

Life history traits of global mammals varied primarily along a two-dimensional space accounting for 75.1% of the total variance (**II**). This space is characterized by two primary trade-offs: litter size versus gestation length (angle of 178° in the reduced space, $r = -0.99$) and number of litters per year versus age at female maturity and weaning length (angle of 175° and 176° , respectively). The first dimension captured the fast–slow continuum, distinguishing fast species with short lifespans, short gestation and weaning periods, early maturity, and frequent litters from slow species with fewer and less frequent litters, longer lifespans, and later maturity (Fig. 4a). The second dimension captured the trade-off between litter size and frequency, reflecting lifetime reproductive effort through offspring quality (*i.e.*, species born in an underdeveloped state versus those born as mature, mobile individuals) and reproductive frequency (*i.e.*, semelparity vs. iteroparity, Fig. 4a). Within this trait space, global mammals are unevenly distributed, forming two hotspots at opposite ends of the fast–slow continuum: those investing in the quantity of reproductive output versus those prioritizing quality (Fig. 4a).

These two global hotspots align with terrestrial (fast hotspot) and aquatic and aerial (slow hotspots) realms' trait structures (**II**), suggesting an environmental realm-driven effect in shaping global mammalian strategies (Fig. 4). Semi-aquatic species exhibit intermediate life history strategies, slower than terrestrial species but faster than fully aquatic ones, in a way that appears related to species' water dependence. Indeed, except for semi-aquatic species ($SES_{\text{semi-aquatic}} = -0.89$; $p = 0.27$), environmental realms showed significantly lower SES than expected by random, indicating high redundancy within each realm ($R_{\text{land}} = 7.99$, $R_{\text{air}} = 9.25$, $R_{\text{water}} = 4.38$, $p < 0.001$), suggesting that each realm favours a constrained set of life history strategies unique to that realm.

Supporting this environmental realm-driven effect on global mammalian strategies (**II**), overlap-based dissimilarities across realms were generally high ($D_{\text{land-water}} = 69\%$, $D_{\text{land-air}} = 86\%$, $D_{\text{air-water}} = 86\%$; $p < 0.001$, Fig. 4b–d), apart from semi-aquatic species, which showed generally low dissimilarity with terrestrial species. These dissimilarities in realm structures were primarily due to differences in the dominant strategies within realms, rather than to a new, exclusive set of strategies in each realm. This means that, despite marked differences in which strategies were highly frequent, the strategies of one realm can still be observed in others. This is particularly evident in the aquatic realm, where life history strategies are fully encompassed by those of terrestrial species ($\text{Nestedness}_{\text{land-water}} = 1$, Fig. 4c), with apes (including humans) sharing similar life history traits with dolphins. The aerial realm also overlaps significantly with the terrestrial realm ($\text{Nestedness}_{\text{land-air}} = 0.89$, Fig. 4b), largely due to arboreal primates like lemurs.

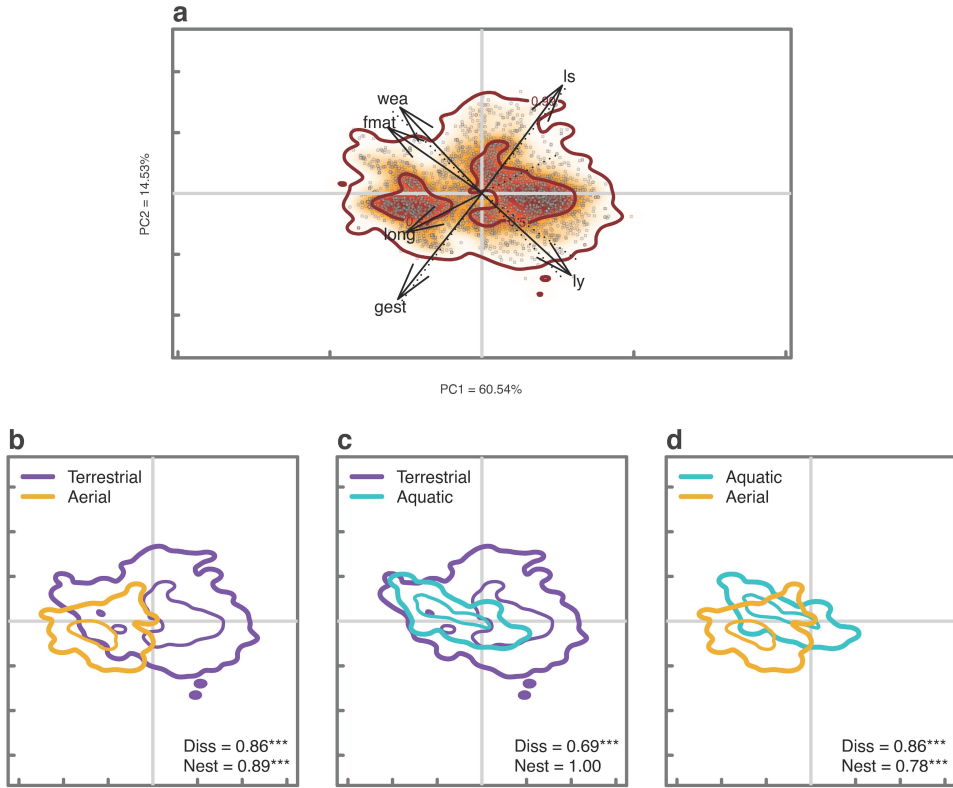


Fig. 4 a: probabilistic species distributions in the space (*i.e.*, trait structure) defined by the two first principal components of PCA considering life history traits for all mammals. Arrows indicate the loadings of each trait in the space. fmat, time to reach female maturity; gest, gestation length; long, longevity; ls, size of litter; ly, number of litters yearly; wea, weaning length. Thick contour lines show the amount of trait space (*i.e.*, functional richness) occupied at 50% and 99% probabilities. The red regions falling within the limits of 50% probability correspond to the hotspots mentioned in the text. **b, c, d:** overlap-based dissimilarities between terrestrial (purple), aerial (light orange), and aquatic (light blue) trait structures in the life history space. Specifically: **(b)** dissimilarity between terrestrial and aerial realms; **(c)** dissimilarity between terrestrial and aquatic realms; **(d)** dissimilarity between aerial and aquatic realms. Each realm is highlighted at 50% (fine lines) and 99% (thick lines) of total probability. SES of dissimilarity and nestedness values for each pairwise comparisons are reported in the legend together with SES p-values (***SES $p < 0.001$). Adapted from paper II Fig. 1 and Fig. 2.

The life history strategies shared across terrestrial, aerial, and aquatic realms were coincident with strategies observed in arboreal, semi-arboreal, and fossorial modes of life (II). Arboreal, semi-arboreal, and fossorial mode of life were associated with distinct life history strategies compared to land-confined species ($D_{\text{land-arboreal}} = 61\%$, $D_{\text{land-semiarboreal}} = 47\%$, $D_{\text{land-fossorial}} = 53\%$; $p < 0.001$ in all cases), with land-confined species primarily clustering in the fast hotspot of life history space. Nestedness between terrestrial and aerial species decreased by 55% (increasing dissimilarity between the realms by 10%) when only land-confined terrestrial species were considered, although these species add up to 66.3% of all terrestrial species. Similarly, dissimilarity between aquatic and land-confined species increased by 15% compared to the dissimilarity computed across the entire spectrum of terrestrial adaptations. Arboreality is the primary reason for these overlaps in the life history space, especially in the case of the aquatic realm, with arboreal and aquatic species sharing more similar life history strategies than arboreal and land-constrained ones ($D_{\text{water-arboreal}} = 55\%$, $D_{\text{land-arboreal}} = 61\%$, $p < 0.001$). This effect of the terrestrial mode of life in expanding the set of strategies available on land suggests a combined influence of environment and modes of life in shaping trait diversity across global mammals.

These findings were consistent regardless of the shared ancestry of mammalian species (II). Within orders, mammals with aquatic or semi-aquatic lifestyles generally exhibited slower strategies than terrestrial species. Similarly, land-confined species generally showed faster strategies than arboreal or fossorial representatives of the same order. All models relating environmental realms or modes of life to species' positions along trait space dimensions (both standard and phylogenetically informed) confirmed the statistical significance of these findings and emphasized their independence from species' evolutionary history.

3.3. Relationships between trait and spectral diversity

In coastal dunes, both trait and spectral structures were strongly and positively related (III). Overall, plots showed higher spectral dissimilarity (mean all plots: 0.68 ± 0.22) compared to trait dissimilarity (0.54 ± 0.21). The Mantel test revealed a positive correlation between the two dissimilarities across the entire study area ($\rho = 0.39$, $p = 0.001$). This relationship was further supported by major axis regression analyses within each transect, which consistently demonstrated positive correlations between trait and spectral dissimilarities (ρ ranging from 0.50 to 0.77, all $p < 0.001$, Fig. 5). Although spectral dissimilarities were generally higher and exhibited lower nestedness than trait dissimilarities, both types of dissimilarity were largely driven by high nestedness (*i.e.*, significant overlap) among plot structures of each transect. This indicates that dissimilarities between plots within the same transect were primarily due to variations in how species and pixels occupied corresponding regions of the trait and spectral spaces, respectively. Furthermore, all major-axis regression models relating functional and

spectral richness showed significant positive associations. The strength of these relationships (R^2 between 0.11 and 0.40) and their slopes varied among transects, indicating a transect-specific effect in shaping the relationships between trait and spectral structure boundaries.

The relationship between trait and spectral structures was further confirmed by the alignment of trait and spectral diversity patterns along the ecological gradient shaping coastal dune communities (**III**). Trait dissimilarities among plots displayed transect-dependent patterns, generally increasing linearly among closer plots and levelling off at higher dissimilarity values in more distant plots (Fig. 5). Spectral dissimilarity also increased with plot distance without reaching a plateau, though the degree of linearity in this relationship varied across transects (Fig. 5). These findings suggest that plots closer along the environmental gradient tend to share similar sets of traits and values, which is reflected in corresponding patterns of spectral band values. However, the saturation of trait dissimilarities at greater plot distances suggests that, depending on the species composition of each transect, adjacent plots can exhibit higher dissimilarities than more distant ones, a pattern not mirrored by spectral dissimilarity. Both trait and spectral richness exhibited a slight decline along the sea-inland gradient, with the degree of this decline varying by transect. This pattern suggests that communities nearer to the sea tend to host species with generally higher trait and spectral diversity. All dissimilarity and richness models demonstrated statistically significant relationships between diversity metrics and the sea-inland gradient.

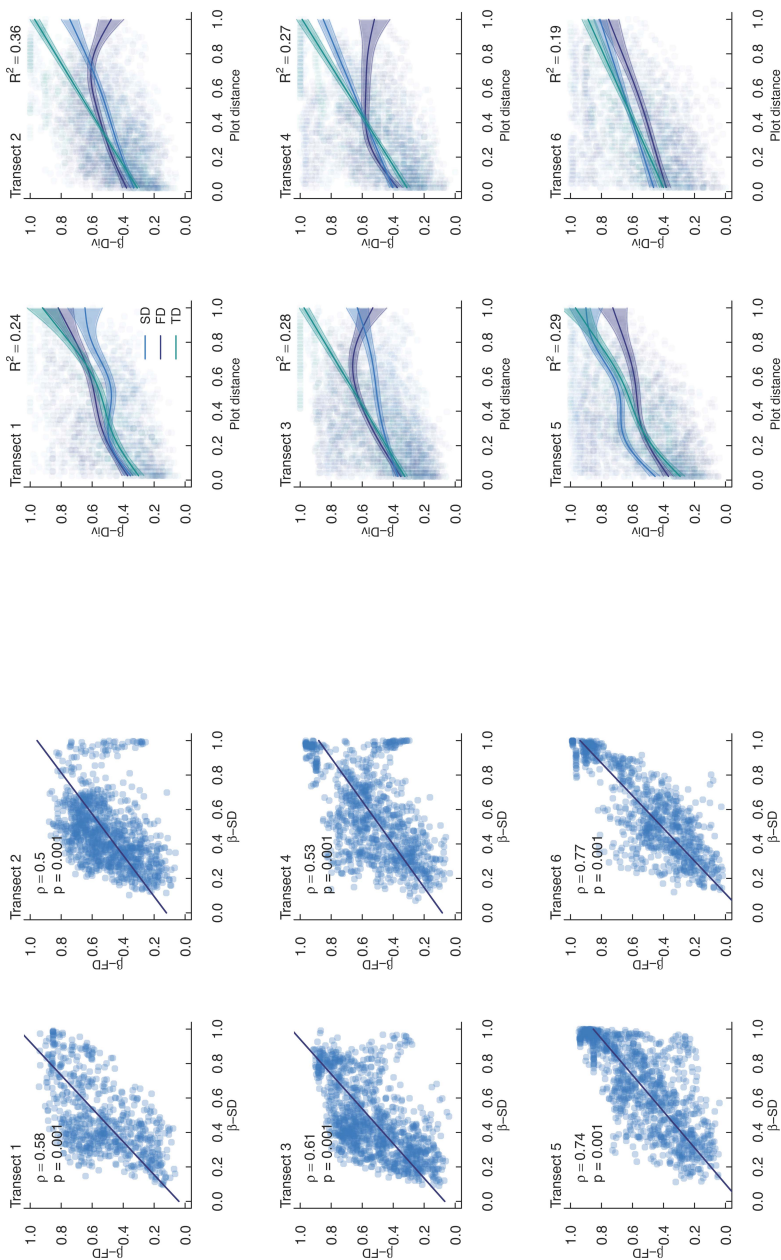


Fig. 5 Left: relationships between transects' spectral (SD) and trait (FD) β -diversity which was calculated as overlap-based dissimilarity across plots' trait structure of each transect. Each panels shows the coefficient of correlation (ρ) and its significance (p ; based on Mantel tests). Right: relationships between taxonomical (β -TD), trait (β -FD), and spectral (β -SD) dissimilarities and plot distances within transects. Panels include fit line and R^2 from generalized additive models relating diversity facets and plot distance. The shaded area corresponds to the 95% confidence interval for each diversity facet (SD: blue, FD: purple; TD: green). For details on taxonomical diversity and its computation refer to paper **III**. Adapted from paper **III** Fig. 2 and Fig. 4.

4. DISCUSSION

In this thesis, I characterized trait spaces for both plants (**I** and **III**) and mammals (**II**), demonstrating the versatility of this tool in addressing and quantifying species diversity patterns (**I**, **II**, **III**) and highlighting its potential application in biodiversity monitoring (**III**). First, by integrating maximum rooting depth and lateral root spread into the UPFS, I showed that above- and belowground size are strongly aligned, forming a single dimension of global trait variation (**I**). Next, by examining patterns in the organization of mammals within the global trait space (**II**), I demonstrated that environmental realms are closely linked to the diversity of life history strategies available in nature, with differences in modes of life expanding the range of strategies. Finally, I demonstrated that trait patterns across plant communities are closely approximated by spectral patterns in pixels from the same communities (**III**), suggesting that insights typically derived from trait diversity analysis in trait spaces can also be effectively captured through remote sensing imagery.

4.1. Dimensionality and trait correlation structures of global spaces

Considering global plants (**I**), I showed that plant size does not modify the dimensionality or structure of the UPFS, supporting the hypothesis of coordination between above- and belowground size traits in global plants. Physiological and geometric constraints imposed by allometric scaling lead to a proportional relationship between above- and belowground biomass across species, independent of phylogenetic affiliation or environmental conditions (Enquist & Niklas, 2002; Smith-Martin et al., 2020; Puglielli et al., 2021). This proportional relationship reflects the fact that larger plants typically require extensive root systems to meet their nutrient and water demands and to stabilize aboveground structures. These large root systems, in turn, require a significant amount of energy for maintenance, which necessitates an extensive photosynthetic area (Schenk & Jackson, 2002). Consequently, incorporating root size traits minimally altered the dimensionality of the UPFS, contrary to the expected effect of adding an uncorrelated trait, instead loading on the same dimension as aboveground size. This finding suggests that global variation in belowground size is effectively represented along the same dimension as aboveground size, supporting the idea that, in line with allometric theory, plants globally follow two broad size investment strategies: either growing large in both above- and belowground components or remaining small.

Highlighting the strength of size investment coordination, the inclusion of root size traits did not alter the fundamental correlation structures of either plant trait subset (**I**). Although adding root size traits did not modify the dimensionality of

the trait space (and thus did not affect the amount of variation in the space), and these traits aligned along the first dimension, their inclusion may have impacted the correlation structure that shapes the ecological identity of the other UPFS dimensions. However, trait angles across the original UPFS showed nearly perfect correlations with angles in trait spaces that included root size traits. Accordingly, the ecological identity of the aboveground (*i.e.*, size and leaf economics, Fig. 3; Díaz et al., 2016; Carmona, Bueno, et al., 2021) and belowground (*i.e.*, root coordination and root collaboration, Fig. 3; Bergmann et al., 2020; Carmona, Bueno, et al., 2021) dimensions remained consistent with the inclusion of root size traits, without modifying our ideas about the set of strategies available for global plants. This finding underscores a key aspect of plant trait dimensionality: while aboveground and fine root traits related to construction costs and resource acquisition vary at a global scale (Carmona, Bueno, et al., 2021), traits defining plant size exhibit remarkable consistency.

Similarly, the strategies available to global mammals are constrained by fundamental trade-offs and coordination pervasive across all mammalian adaptations (**II**). Mammals balance the costs associated with longevity and offspring survival by reducing either the frequency or magnitude of reproductive output, depending on whether they emphasize prenatal (*i.e.*, longer gestation) or postnatal (*i.e.*, extended weaning) investment (Fig. 4; Stearns, 1992). From polar regions to deserts, producing offspring better adapted to their environment at birth requires energetic investments in longer gestations, at the expense of the number of litters a mother can bear. Likewise, maternal investment in gradually guiding offspring to independence enhances survival but results in fewer litters per year. These trade-offs are confirmed at a global scale by trait angles in the reduced trait space and define the two main dimensions of life history variation: the pace of life, ranging from fast to slow strategies, and lifetime reproductive effort. This consistency in the limited set of strategies exhibited by both mammals and plants underscores the universal nature of trade-offs and coordination, arising from inescapable physical and biological constraints across organisms (Elgar & Harvey, 1987; Enquist & Niklas, 2002; Burger et al., 2021; Junker et al., 2022).

4.2. Mammalian structure in the trait space

Global mammals cluster in two main hotspots within the trait space, indicating that despite diverse adaptations (Fig 4a), life history strategies are largely dichotomized based on the environmental realms they inhabit (**II**). Aerial and aquatic mammals occupy the slow hotspot, adopting strategies that enhance offspring survival through long-term distribution of reproductive effort. In contrast, terrestrial species cluster in the fast hotspot, favouring rapid gene propagation through short-term reproductive efforts. Accessing aerial and aquatic realms requires costly morpho-physiological adaptations, which demand increased parental investment to prepare offspring for these physically demanding environ-

ments (Perrin et al., 2009; Barclay & Fleming, 2020). For instance, the energetic demands of water on both mother and offspring compel the rationing of resources through delays in offspring maturity and the mother's successive births (Perrin et al., 2009; Davis, 2019). Similarly, the longevity associated with flight demands specialized structures and size, extending gestation and weaning while allowing relatively frequent reproduction due to lower maternal energetic costs compared to aquatic species (Barclay, 1994; Barclay & Fleming, 2020). This environmentally driven selection in global mammalian patterns is further evidenced by high levels of trait redundancy within realms (II), indicating realm-specific convergence around similar trait values. Additionally, the high overlap-based dissimilarity across realms, confirmed even after accounting for phylogenetic relatedness, supports this pattern (Fig. 4b–d). This bimodal trait distribution mirrors patterns observed in plant strategies for aboveground resource allocation (Díaz et al., 2016; Carmona, Bueno, et al., 2021), where species converge around a few contrasting syndromes that support successful strategies (Junker et al., 2022). Environmental pressures strongly influence this selection process (Joswig et al., 2022) appearing to operate independently of evolutionary history in mammals (II) but not in plants (I; Capdevila et al., 2023).

Despite marked differences among environmental realms (II), differences in mode of life expanded the set of strategies available on land, suggesting that ecological adaptations could enable species to adopt otherwise less favoured life history strategies in a realm. With varying extents, the arboreal, semiarboreal, and fossorial modes of life enable species to evade mortality risks and access new ecological opportunities (Scheffers et al., 2017; Bels & Russell, 2023). This reduction in mortality resulting from the vertical exploitation of land (Shattuck & Williams, 2010; Healy et al., 2019) allows to modify pressures acting on species, thereby expanding the extent of terrestrial trait structure. Consequently, while the environmental realm in which species live seems to drive life history strategies, species mode of life seems to modify the environmental pressures perceived on land, expanding the diversity of strategies exploitable in the terrestrial realm.

4.3. Integrating trait spaces into remote sensing frameworks

Remote-sensing approaches enable affordable and continuous biodiversity estimations over large areas, which are essential for addressing ongoing global changes (Jetz et al., 2016; Reddy et al., 2021). By examining the spectral structure of plant communities along an ecological gradient (III), I demonstrated that the same holistic diversity measurements obtained from trait spaces (as in I and II) can be derived remotely, potentially easing trait diversity monitoring under global change scenarios. Spectral diversity strongly corresponded to trait diversity across communities, both in the extent of trait/spectral structures and in overlap-

based dissimilarity (Fig. 5), indicating that shifts in community traits are reflected in band value changes.

However, the strength of the relationship between spectral and trait diversity was highly transect-dependent (III). This variability likely arises from differences in sampling resolution between trait and spectral data. Collecting trait data is time-intensive (Homolova et al., 2013) and limited by the number of species sampled, replicates per individual, and selected traits, all of which shape the trait space being studied. In contrast, remote sensing can capture the full set of traits influencing the spectral signal of each individual within an image, depending on the spatial and spectral resolutions of the images (Wang & Gamon, 2019; Cavender-Bares et al., 2020). In this study, variation in plot spectral structures reflects species presence, abundance, and interspecific variability across the complete set of features defining each individual's spectral signature, providing a snapshot of underlying individuals with multiple replicates based on individual size. Conversely, trait measurements were limited to species-level averages of the most abundant species. Thus, plots containing the same species but situated at different points along the sea–inland gradient may exhibit interindividual differences that are detectable only through spectral structure, not through trait structure. This may potentially contribute to varying R^2 values across transects. Despite these resolution differences, the way spectral diversity mirrors trait diversity patterns (both in functional richness and dissimilarity) along the ecological gradient suggests that spectral diversity is a reliable proxy for community trait structure and may serve as a robust indicator for a fast monitoring of trait diversity. I suggest future research to further validate this relationship across different habitats and spectral resolutions.

5. CONCLUSIONS

In this thesis, I applied trait spaces to explore patterns and processes shaping plant (I) and mammalian (II) diversity, and to test whether spectral diversity can approximate the level of detail provided by multifaceted trait diversity assessments (III). Specifically:

- I. Through the inclusion of root size traits in the UPFS, I demonstrated that plant size defines a single continuum of allometric investments at the global scale, independent from leaf and root economic strategies.
- II. I demonstrated that, similar to plants, global mammalian life history strategies cluster into two high-density hotspots, representing investments in fast and slow life paces. Furthermore, I found that major environmental realms were strong predictors of mammalian life history strategies, each selecting for a unique set of life history adaptations. Additionally, I demonstrated that different modes of life expanded the diversity of life history strategies otherwise favoured on land.
- III. I demonstrated that, by analysing spectral diversity within the same framework used for trait spaces, it was possible to remotely approximate various aspects of trait diversity, thereby capturing trait patterns across plant communities.

However, a note of caution is warranted. While trait spaces provide a valuable foundation for extracting organisms strategy (I, II), assessing environmental and ecological drivers of trait variation (II), and measuring trait patterns across spatial scales (III), there are inherent limitations to this approach that must be kept in mind. Trait spaces are heavily dependent on the set of species and traits included, a factor that is particularly important when addressing global trait spaces, which rely on available datasets.

Notably, more than 64% of known plant diversity is unrepresented in global trait datasets (I), with databases disproportionately biased toward the global North (Cornwell et al., 2019; Maitner et al., 2023). Similarly, only 54% of currently recognized mammalian species have partial trait measurements (II, Burgin et al., 2018). Consequently, while global diversity frameworks serve as a fundamental baseline for trait-based ecology (Laughlin, 2014; Mouillot et al., 2021), they are strongly limited by species representation biases. This underscores the need to integrate under-sampled species and biomes to fully understand global strategies and patterns in the community assembly of plants and mammals.

Furthermore, it is essential to continually update trait spaces by including overlooked traits related to fundamental investments of species. For instance, clonality-related traits correlate with aboveground size in herbaceous plants (Klimešová et al., 2021; Chelli et al., 2024), suggesting a possible role of clonality in influencing covariation between above- and belowground biomass investments (I). Similarly, dietary, migratory, and social habits correlate with different

mammalian life history traits (Famoso et al., 2018; Soriano-Redondo et al., 2020; Zhu et al., 2023), and may relate to patterns of life history diversity and species distribution within mammalian space (II). As data on these traits become more widely available, it is crucial to update global frameworks to include overlooked species and missing traits. Yet, the findings of this thesis provided fundamental insights into plant and mammalian adaptations, establishing a foundation for further exploration of ecological and evolutionary processes. This foundation may enhance our understanding of the drivers and consequences of ongoing global changes and future biodiversity patterns.

As we confront these challenges, I further demonstrated that spectral diversity has the potential to approximate all aspects of trait diversity remotely (III), if it is analysed with a consistent analytical framework. Furthermore, the mismatch observed across transects between trait and spectral variation likely arises because the spectral signal captures both intra- and interindividual differences. Since this level of sampling detail is not always achievable with trait data, spectral diversity emerges as a powerful surrogate for estimating the trait structure of plant communities in a fast, repeatable manner across broad spatial scales, while accounting for the relative contribution of intraspecific trait variability. Altogether, this thesis further proves the fundamental versatility of trait spaces in disentangling and studying biodiversity.

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SUMMARY IN ENGLISH

In this thesis, I investigate how the use of trait spaces offers a structured approach to understanding and analysing the diversity of plant and mammalian species. Trait spaces are mathematical tools that map the vast range of traits organisms exhibit, enabling researchers to extract patterns in ecological strategies and quantify diversity at various levels of ecological and spatial organization. By distilling the myriad forms and functions of organisms into manageable dimensions, trait spaces facilitate the exploration of how different species interact with each other and their environments, providing fundamental tools to explore the drivers and processes behind organismal assembly. This method is increasingly vital in an era of rapid environmental change, where human activities are altering ecosystems, impacting biodiversity, and accelerating species extinction. Understanding the underlying drivers of these ecological shifts requires a system to compare and quantify traits, offering insight into the eco-evolutionary processes that shape global biodiversity.

Accordingly, in this thesis, I develop a framework to test whether the inclusion of root size alters the dimensionality and structure of global plant strategies (I), potentially modifying the known diversity of global plant strategies. Given the lack of comprehensive information on global mammalian trait diversity, I then produce a global space summarizing mammalian life history diversity, which I use to explore whether environmental realms (*i.e.*, water, air, land) and modes of life (*e.g.*, arboreality, fossoriality) influence global patterns of mammalian trait diversity (II). Lastly, I test whether the trait diversity of plant communities, encompassing all its multivariate components, can be detected remotely (III). Specifically, I assess whether spectral diversity can serve as a reliable proxy for the rapid and extensive extraction of trait diversity patterns.

In the global analysis of plant strategies (I), I include rooting depth and lateral spread in a set of ten traits known to define fundamental aboveground and fine-root investments. Results demonstrate that root size traits do not alter the known fundamental structure and dimensionality of global plant trait space. Confirming allometric scaling predictions, root size traits align along a single continuum with aboveground size, independently of leaf and root economic strategies. This unified size dimension refines plant trait diversity analysis by showing that global plant strategies are organized around core size investments, balancing above- and belowground growth in ways that appear independent of leaf and root economics.

The analysis of mammalian life histories (II) reveals that global investments in growth, survival, and reproduction are highly constrained and can be summarized by two main dimensions of trait variation. Within these dimensions, there is a clear separation between species prioritizing rapid reproduction and shorter lifespans (fast-paced strategies) and those emphasizing longevity with lower reproductive output (slow-paced strategies). These strategies are significantly shaped by the environmental realms mammals inhabit, with aquatic and aerial realms favouring slow-paced strategies and the terrestrial realm predominantly

favouring fast-paced strategies. Results further suggest that modes of life expand the diversity of terrestrial strategies, suggesting a possible interplay of ecological adaptations and environmental drivers in shaping strategies available within each realm. Together, these findings highlight how environmental constraints drive distinct adaptations and shape trait diversity within global mammals, emphasizing the strong relationship between environmental realms and life history evolution.

Finally, I demonstrate the potential of spectral diversity, derived from remote sensing, to serve as a proxy for plant trait diversity along environmental gradients (III). By analysing coastal dune plant communities, I show that spectral diversity, measured through high-resolution multispectral imagery, effectively mirrors the patterns of trait diversity observed on the ground. The strong correspondence found between trait and spectral patterns in spatial occupation and along environmental gradients suggests that remote sensing can capture complex ecological information quickly and across large areas, offering a promising approach for biodiversity monitoring, especially under conditions of rapid environmental change.

In conclusion, the results of this thesis highlight the versatility of trait spaces as essential tools for organizing and interpreting global biodiversity patterns across plants and mammals. By synthesizing trait diversity through key dimensions of trait covariation, these frameworks reveal how trade-offs and coordinated energetic investments are pervasive in plants and animals. Such constraints limit the set of strategies available to global species, with the environment strongly selecting which strategies are more frequent under specific environmental conditions. The successful integration of spectral diversity as a proxy for trait diversity further underscores the potential of remote sensing for large-scale biodiversity monitoring, offering a means to address the same multivariate features measurable through trait spaces in a fast and repeatable way. Together, these studies provide a structured approach to understanding species strategies, supporting both theoretical-ecological insights and practical applications in conservation amid accelerating environmental change.

SUMMARY IN ESTONIAN

Erinevate elustikurühmade tunnusruumide kaardistamine ja uurimine

Ökoloogilised ja evolutsioonilised protsessid on põhjustanud erinevate elustikurühmade erakordse mitmekesisuse. See mitmekesisus omakorda kindlustab ökosüsteemide toimimise ja pakub hüvesid inimestele, kuid praeguses kiirete keskkonnamuutuste ajajärgus on inimtegevuse tõttu ökosüsteemid muutumas ja elurikkus vähenemas. Olukorraga toimetulemiseks vajame järjest rohkem teadmisi sellest, millised tunnused tagavad elusorganismide püsimise ökosüsteemis. Funktsionaalsed tunnused – morfoloogilised, füsioloogilised, ehituslikud, fenoloogilised või käitumuslikud omadused, mida saab indiviidi tasandil mõõta – määravad, kuidas organismid keskkonnale reageerivad ja seda mõjutavad. Kuna mõõdetavaid tunnuseid on palju ning need erinevad elustikurühmade vahel, siis on vajalik kasutada ühtset süsteemi, mis võimaldaks tuvastada liikide ökoloogilisi strateegiaid ning hinnata ja võrrelda elurikkust erinevatel ökoloogilistel ja ruumilistel tasanditel. Tunnusruumid on matemaatilised tööriistad, mis kaardistavad organismide tunnuste mitmekesisuse mitmemõõtmelises ruumis, võttes arvesse mõõdetud tunnuste omavahelisi seoseid. Ruumi iga telg moodustab pideva skaala, millele saab paigutada organisme vastavalt nende tunnuste või tunnuste kombinatsioonide väärtustele, nii et funktsionaalselt sarnased organismid asetsevad üksteisele lähemal. Kuna tunnusruumid lähendavad organismide eluvormide ja talitluste mitmekesisuse lihtsasti hallatavateks mõõtmeteks, siis hõlbustavad need liikide vastasmõjude ja keskkonnaseoste uurimist.

Käesolevas doktoritöös uurisin, kuidas tunnusruumide abil saab paremini mõista, analüüsida ja monitoorida taimede (I, III) ning imetajate (II) elurikkust. Minu peamised eesmärgid olid 1) laiendada globaalset taimede tunnusruumi, kaasates juure suuruse tunnused (I); 2) luua terviklik imetajate tunnusruum ja uurida, kuidas loomade elukeskkond ja eluviis mõjutavad nende strateegiaid (II); 3) hinnata, kas kaugseire teel saadud taimkatte piltide spektraalribade mitmekesisus (spektraalne mitmekesisus) võiks olla usaldusväärne vahend tunnuste mitmekesisuse kiireks ja ulatuslikuks kaardistamiseks (III).

Globaalset taimede tunnusruumi on varasemalt kirjeldatud nii kuue maaapealse tunnuse kui ka nelja peenjuure tunnuse abil. Maaapealsed tunnused moodustavad kaks sõltumatut telge, mis kirjeldavad peamisi taimestrategieid ja on seotud taime suuruse ning lehtede ökonoomikaga (ressursi hankimine ja säilitamine). Maa-alused peenjuure tunnused taanduvad samuti kahele teljele, mis peegeldavad juurte vajadust ja võimalust mükoriisa moodustamiseks ning juurte ökonoomikat. Hilisemad püüded ühendada taimede maaapealsed ja -alused tunnusruumid on andnud vastakaid tulemusi ning kogu taime funktsionaalsete strateegiade ülevaade vajab veel uurimist. Eriti on välja toodud vajadust lisada tunnusruumi ka taime maa-alused mõõtmed. Oma doktoritöös püüdsingi luua kogu taime tunnusruumi, kasutades olemasolevaid taimetunnuste andmestike ning kaasates juurestiku sügavuse ja horisontaalse ulatuse tunnused (I). Tulemused

näitasid, et juurestiku suuruse tunnused ei muuda teadaolevat taimede tunnusruumi struktuuri ega mõõtmelisust. Globaalse taimede tunnusruumi kirjeldamiseks on vaja nelja sõltumatut telge. Juurestiku suuruse tunnused joonduvad maapealse taime suuruse tunnustega ühele teljele, sõltumata lehtede ja juurte ökonoomikast. Seejuures ei ole taimeliigid sel teljel ühtlaselt jaotunud vaid järgivad vastavalt allomeetrilise kasvu teooriale kahte peamist suurusesse investeerimise strateegiat: kasvavad suureks nii maapealsetes kui ka maa-alustes osades või püsivad väikesed.

Kui taimede tunnusruumi uurimine on oluliselt edenenud, siis loomade jaoks ei ole sarnast globaalset raamistikku veel välja töötatud. Siiski on viimastel aastatel järjepidevalt koostatud ja täiendatud imetajate tunnuste ülemaailmseid andmebaase. Kasutades olemasolevaid andmeid ning puuduvate tunnuste imputeerimist (fülogeneetilisel lähedaste liikide tunnustel põhinev hinnang) moodustasin globaalse imetajate tunnusruumi (II). Imetajate kuuel elukäigutunnusel põhinev analüüs näitas, et kasvu, ellujäämisse ja paljunemisse tehtud investeeringud on imetajate puhul tugevalt piiratud ja kõiki uuritud tunnuseid saab kokku võtta kahe peamise mõõtmena. Esimene mõõde eristab liigid, kes on lühema elueaga ja saavutavad kiirelt suguküpsuse (kiire strateegia), ning liigid, keda iseloomustab pikaalalisus ja hiline suguküpsus (aeglane strateegia). Teine mõõde kajastab järglaste arvu ja paljunemise kiiruse tunnuseid, mis peegeldavad imetajate iteropaarset (elu jooksul mitu korda paljunev) ja semelpaarset (üks kord paljunev) elustrateegiat. Kiire-aeglane strateegia on tugevalt mõjutatud imetajate elukeskkonnast – kui vees ja õhus elamine soosib aeglaseid strateegiaid, siis maismaal on edukamad kiire strateegiaga liigid. Lisaks leidsin, et maismaa imetajad hõlmavad suurema osa tunnusruumist kui vees või õhus elavad loomad, sest erinevad eluviisid (nt arborikool ehk puudel tegutsev või fossoor ehk kaevuv) võimaldavad liikidel vältida keskkonnast tulenevaid ohte ja hõivata rohkem ökoloogilisi nišše.

Globaalsed tunnusruumid annavad olulisi alusteadmisi liikide strateegiate evolutsiooni ja biogeograafia kohta, kuid tunnusruumide rakendamine koosluse tasandil aitab välja selgitada, millised ökoloogilised protsessid tagavad elurikkuse ja ökosüsteemide toimimise. Kiirete keskkonnamuutuste tingimuses on oluline ka, et elurikkust saaks mõõta ja monitoorida suurel alal ühtlaselt ja kiiresti. Kaugseire pakub sellele väljakutsele paljulubava lahenduse, kuna taimede morfoloogiliste, füsioloogiliste ja keemiliste tunnuste varieeruvus põhjustab fenotüübilisi erinevusi, mis kajastuvad kaugseire piltidel erinevate spektraalribade väärtustena. Seega saab spektraalribade mitmekesisuse (spektraalse mitmekesisuse) uurimisel ajas ja ruumis aimu taimekoosluse taksonoomilisest ja funktsionaalsest mitmekesisusest. Varem on kaugseiret seostatud üksikute taimetunnuste või limiteeritud mitmekesisuse näitajatega, kuid oma doktoritöös ühendasin kaugseire andmed ja tunnusruumi metoodika, et uurida spektraalse mitmekesisuse potentsiaali taimetunnuste mitmekesisuse hindamiseks keskkonnagradiendil (III). Kuna tunnusruumi metoodikat saab rakendada ka teistele andmetele, siis lõin nii spektraalse mitmekesisuse „tunnusruumi“ kui ka Itaalia Toscana rannikuluidete

taimekoosluste tunnusruumi ning uurisin nende ruumitelgede omavahelisi seoseid. Tulemustest selgus, et spektraalne mitmekesisus kajastab tõhusalt koosluses mõõdetud tunnuste mitmekesisuse mustreid. Kaugseire võimaldab kiiresti ja ulatuslikult haarata keerulist ökoloogilist teavet, pakkudes lootustandvat lähenemist elurikkuse monitoorimiseks.

Minu doktoritöö tulemused näitasid, et tunnusruumid on mitmekülgsed ja olulised tööriistad globaalse elurikkuse võrdlemiseks ja uurimiseks nii taimede kui ka imetajate puhul. Tunnuste mitmekesisuse taandatavus peamistele strateegiatele näitab, et tunnustevahelised lõivsuhted ja energiaetilised piirangud on levinud nii taimede kui ka loomade seas. Sellised piirangud kitsendavad globaalsel skaalal võimalikke strateegiate kombinatsioone, kusjuures keskkond määrab väga tugevalt, millised strateegiad on teatud tingimustes sagedasemad. Lisaks näitab spektraalse ja tunnuste mitmekesisuse tugev seos kaugseire võimekust elurikkuse monitoorimisel suurel skaalal. Tunnusruumi meetodika kasutamine pakub ühtset lähenemist liikide strateegiate mõistmiseks nii ökoloogia teooria küsimustes kui ka praktilistes rakendustes looduskaitstes.

ACKNOWLEDGMENTS

I was fortunate to get an early glimpse of what my future as a PhD student in Tartu might look like. During my time in Estonia at the end of 2019 for my master's thesis, I had the opportunity to work with Carlos, meet most of the members of the Botany Department, and experience life in Tartu, including our workplace at the time, the Botanical Garden. Science was great, people were nice. However, as a loud person who had never lived outside the chaos of an Italian city, I found Tartu and its people to be too quiet and a bit cold, like Estonian winter. For this reason, I accepted the PhD position sure that this decision would mean sacrificing a part of my life at the altar of science. A PhD position in Tartu meant great science and great scientific examples, yet I knew that my way of living and interacting with others would inevitably be challenged in this quiet, introverted, Nordic landscape.

Now, at the end of this journey, I can say that I was clearly mistaken in predicting the outcome, with my perception likely influenced by the different ways in which cultures communicate. Let's be clear: I faced my share of struggles and moments of discord as I tried to fit in, especially in the beginning, along with several cultural shocks—like the soft, direct, and concise tone of conversations, the quiet grace with which people would disappear from gatherings without a word, the effortless ease of sharing a sauna, naked, with the very same individuals evaluating my PhD progress. Yet, in the end, I found that all these peculiar customs and habits gradually became a natural part of my life, with many even becoming a welcome novelty. More importantly, I discovered that pursuing a PhD in Estonia was not a sacrifice but rather a necessary evolution. It strengthened and sharpened some of my core characteristics while broadening the naturally limited perspective of someone who had never truly experienced life beyond her own country. I am grateful to all those who crossed my path during these years for that.

Therefore, leveraging the main topic of this thesis, I aimed to provide a lasting snapshot of the diversity of individuals who shaped my PhD experience. To achieve this, I invited those who defined my social environment during this time to complete a test from www.16personalities.com, which measures five continuous traits reflecting aspects of individual personality. Using these traits, I constructed a Tartu personality space and I analysed patterns in individuals distribution in the space, applying the same framework used in Paper II.

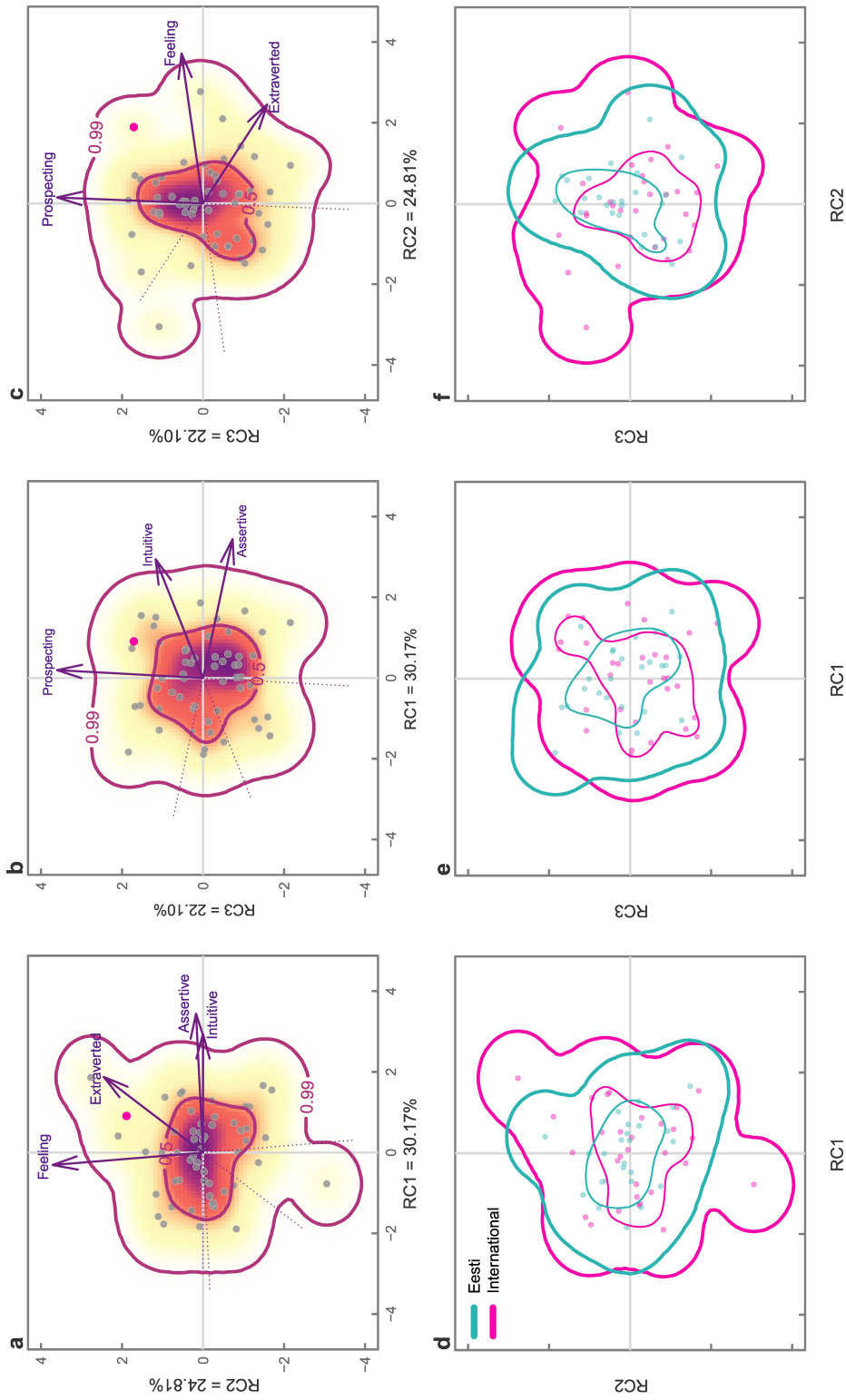


Fig. 6 Tartu personality trait space required three main dimensions to capture the variation in Tartu personality. The first dimension represented the interplay of assertive and intuitive traits, forming a gradient from self-assured, imaginative, personalities to more concrete, success-driven individuals who are, nonetheless, more prone to self-doubt. The second dimension counterpose feeling and thinking personalities, reflecting the extent to which individuals prioritize emotions or rationality when making decisions, and, to a lesser degree, incorporated the extroverted-introverted spectrum. The third dimension illustrated a continuum between prospecting and judging personalities, highlighting the tactics people use to plan and navigate the options available to them. Principal components were Varimax-rotated to enhance the interpretability of the dimensions. The variance explained by each rotated component (RC) is indicated in parentheses, with the total variance explained by the space amounting to 77.62%. Panels **a**, **b**, and **c** illustrate the probabilistic distribution of individuals within the personality space. The colour gradient represents different densities, with darker areas indicating a higher concentration of individuals. Arrow lengths correspond to the loadings of the traits that define the dimensions of the space. Only loadings above 0.5 in at least one dimension are shown in the panel. The pink dot marks my position within this personality space. Panels **d**, **e**, and **f** compare trait structures between Estonian (light blue) and International (pink) personalities across the three dimensions of the space. In all panels, personality structures are outlined at 50% (fine lines) and 99% (thick lines) of total probability. The figure is printed horizontally and should be viewed by tilting the page sideways.

Results suggested that the sense of disconnection I experienced in 2019, when I first moved away from my familiar environment, could be attributed to the averagely high dissimilarity between my personality and those of the people around me (Fig. 6, average dissimilarity = 47%, range = 22%–80%). However, this effect did not appear to be specifically linked to Estonian personalities. Unexpectedly, my personality showed greater dissimilarity with Italian representatives living in Tartu (average dissimilarity = 54%) than with Estonians (average dissimilarity = 43%). Furthermore, when comparing the trait structure of Estonians ($N = 25$) with that of the diverse nationalities represented in Tartu and its university ($N = 30$), no statistically significant differences were found (Dissim. = 58%, p -value = 0.28) with personality structures being highly nested (Nest. = 74%, Fig. 6). These findings challenge my initial impression from 2019, as they suggest that, while Estonians are more clustered in the space than expected from a random distribution of individuals ($SES_{\text{FunctionalRichness}} = -2.18$, p -value < 0.05), the clustering is less pronounced than anticipated and is not strongly linked to Introverted traits. Instead, the personalities of individuals from a single, small country like Estonia showed a significant overlap with the personality structure of a diverse set of international individuals, representing 15 nationalities spanning from Brazil to Sri Lanka to Japan. Indeed, the international group exhibited the most extreme personalities within the space, with significantly more diverse personalities than expected by chance ($SES_{\text{FunctionalRichness}} = 2.06$, p -value < 0.05), thereby expanding the overall diversity of Tartu's personalities. Altogether, these results highlight how first impressions can be biased

when encountering an environment different from the one you grew up in. They also suggest that a highly diverse social environment, like the international one I experienced during these years, functions much like a highly biodiverse ecosystem: it fosters complex interactions and creates unique social niches, promoting opportunities for specialization and personal evolution. This diversity was crucial for me and remains fundamental for everyone, driving not only scientific innovation but also fostering personal development.

This lengthy text is simply a playful way to express my gratitude to all the people who shaped my environment during these years, and, also, an excuse to avoid writing more personal Acknowledgments. I do not feel comfortable publicly sharing my deepest feelings, as I believe they are meant solely for the individuals they are directed to. Yet, I want to mention a few important names for the sake of records, as they were fundamental to me during these years. Obviously, I want to thank Carlos for showing me what real determination and resilience are and, more importantly, for proving that no matter how many rejections you face, if you dedicate yourself fully and pour your passions into your work, success may still come—even if you are a Grimmione. Thanks to Elisabeth, Bruno, Diego, Slendy, Blanca, Juni, Riin, Oscar, Aurele, Yiming, Siqiao, Ayesh, Inga, Tanel, Kadri, Siim-Kaarel, Ali, Elvi, Iris, Marianne, Sanni, Toivo, Jing, the friends of the department, and to Pava, Ricky, Ivan, Giacomo, Joshua, Linda, Leo, Kaisa, Jessica, and all the other friends who provided warmth, fun, shared meals and nights, and all the colour that made Tartu feel like home. Thanks to the Macroecology workgroup and to Meelis, who were my first interaction with both the Estonian world and the high-level science. Most importantly, I want to thank my family. Grazie Enrico per aver condiviso la vita in questi anni. Grazie mamma, papà, Lollo, e tutti gli altri, per essere quello che siete e per avermi sempre dato tutto quello di cui avevo bisogno. Questo è per tutti voi, senza di voi non sarei qui.

‘It’s a dangerous business, [Frodo], going out your door. You step onto the road, and if you don’t keep your feet, there’s no knowing where you might be swept off to.’

‘All that is gold does not glitter, Not all those who wander are lost [...].’— J.R.R. Tolkien

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PUBLICATIONS

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Book chapters:

Carmona, C. P., De Bello, F., **Beccari, E.**, & Mason, N.W.H. (2024) *Functional Diversity Measures*. In Samuel M. Scheiner (ed.), *Encyclopedia of Biodiversity* – 3rd Edition (Vol. 5, pp. 518–532). Elsevier.
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Teaching:

2024 Data analysis in Community Ecology (3 ECTS), University of Tartu.
Lecturing and supervision of the practical part of the course.

Scholarships:

- 2023 Estonian doctoral school short-term mobility grant, Doctoral school of Earth Sciences and Ecology of the University of Tartu, Estonia (1500 €).
2022 IAVS travel grant, International Association for Vegetation Science (999 €).
2022 DORA Pluss activity 1.1. – Short-term mobility, University of Tartu (1240 €).
2019 Borsa di Mobilità Extra ERASMUS – International mobility grant for outgoing students, University of Trieste (1500€).

Awards:

- 2023 Young Community Ecologist Award, best young scientist presentation, 4th International Conference on Community Ecology, Trieste.
2022 Third prize ‘2-minute talk competition’, final conference of the Centre of Excellence EcolChange – Ecology of Global Change: Natural and Managed Ecosystems.
2022 Best oral presentation at the doctoral student conference of the Department of Botany, University of Tartu.

Oral presentations at international conferences (presenting author is underlined):

Beccari, E., & Carmona, C.P. *Plant size: unifying Above and belowground dimensions*. 66th Annual Symposium of International Association for Vegetation Science. 16th–20th September 2024, Funchal, Madeira.

Tordini, E., **Beccari, E.**, Fujinuma, J., Caleño Ruiz, B. L., Tamme, R., Toussaint, A., Trindade, D. P. F., Carmona, C. P. *The hitchhiker’s guide to trait imputation: empirical insights from vascular plants*. 66th Annual Symposium of International Association for Vegetation Science. 16th–20th September 2024, Funchal, Madeira.

Beccari, E., Capdevila P., Salguero-Gómez, R., & Carmona, C.P. *Mammalian life history strategies are strongly associated with environmental realms*. 11th Biennial Conference International Biogeography Society. 7th–11th January 2024, Prague, Czech Republic.

Beccari, E., Capdevila Lanzaco P., Salguero-Gómez, R., & Pérez Carmona, C. *Environment drives the position of mammalian species in the global spectrum of life histories*. 4th International Conference on Community Ecology. 20th–22nd September 2023, Trieste, Italy.

Petruzzellis, F., Bacaro, G., **Beccari, E.**, Castello, M., Maccherini, S., Nardini, A., Pavanetto, N., Puglielli, G., Savi, T., Tomasella, M., Tonet, V., Tordoni, E. *Coordination between water-related traits and the leaf economic spectrum*. 4th International Conference on Community Ecology. 20th–22nd September 2023, Trieste, Italy.

Beccari, E., Pérez Carmona, C., Tordoni, E., Petruzzellis, F., Martinucci, D., Casagrande, G., Pavanetto, N., Rocchini, D., D’Antraccoli, M., Ciccarelli, D. & Bacaro, G. *The devil is in the details: plant spectral diversity from high-resolution imagery captures taxonomic and functional diversity facets in coastal dune communities*. 64th Annual Symposium of International Association for Vegetation Science. 27th June –1st July 2022, Madrid, Spain.

Other scientific activities:

Reviewer for the following journals [n° revisions]: Ecological Indicators [1], Ecography [1], Ecological Monograph [1], Journal of Vegetation Science [2], New Phytologist [1], OIKOS [1].

Member of the organizing committee of the thematic session: *TS(2)15. Expanding the frontiers of trait-based ecology: novel applications across taxa and scales*, III SIBECOL & XVII AEET MEETING, 2nd–7th June 2025, Pontevedra, Spain.

Non-indexed publication: Beccari, E. (2021). *Valutazione della diversità funzionale vegetale da immagini multispettrali ad alta risoluzione: un caso studio sull’ecosistema dunale tirrenico*. Notiziario della Società Botanica Italiana 5, p. 269.

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Haridus:

2020–... Doktoriõpe botaanikas ja mükoloogias, Tartu Ülikool, Eesti.
2017–2020 Magistrikraad (110/110 cum laude) globaalse muutuse ökoloogias, Trieste Ülikool, Itaalia.
2012–2017 Bakalaureusekraad bioloogiateadustes, Bologna Ülikool, Itaalia.

Töökogemus:

2024 Funktsionaalse ökoloogia spetsialist, Tartu Ülikool, Eesti.

Peamised uurimisteemad:

Makroökoloogia, taimede ökoloogia, loomade ökoloogia, tunnustepõhised lähened, elurikkus.

Publikatsioonid:

Beccari, E. & Carmona, C.P. (2024). Aboveground and belowground sizes are aligned in the unified spectrum of plant form and function. *Nature Communications*, 15, 9199. <https://doi.org/10.1038/s41467-024-53180-x>

Beccari, E., Capdevila, P., Salguero-Gómez, R. & Carmona, C.P. (2024). World-wide diversity in mammalian life histories: Environmental realms and evolutionary adaptations. *Ecology Letters*, 27, e14445. <https://doi.org/10.1111/ele.14445>

Beccari, E., Pérez Carmona, C., Tordoni, E., Petruzzellis, F., Martinucci, D., Casagrande, G. et al. (2024). Plant spectral diversity from high-resolution multispectral imagery detects functional diversity patterns in coastal dune communities. *Journal of Vegetation Science*, 35, e13229. <https://doi.org/10.1111/jvs.13239>

Puglielli, G., Bricca, A., Chelli, S., Petruzzellis, F., Acosta, A.T.R., Bacaro, G., **Beccari, E.**, et al. (2024). Intraspecific variability of leaf form and function across habitat types. *Ecology Letters*, 27, e14396. <https://doi.org/10.1111/ele.14396>

Prada, F., Musco, L., Alagna, A., Agnetta, D., **Beccari, E.**, D'Anna, G., et al. (2019). Anthropogenic impact is negatively related to coral health in Sicily (Mediterranean Sea). *Scientific Report* 9, 13469. <https://doi.org/10.1038/s41598-019-49713-w>

Raamatute peatükid:

Carmona, C. P., De Bello, F., **Beccari, E.**, & Mason, N.W.H. (2024). *Functional Diversity Measures*. Samuel M. Scheiner (toim.), *Encyclopedia of Biodiversity – 3rd Edition* (Vol. 5, lk 518–532). Elsevier. <https://doi.org/10.1016/B978-0-12-822562-2.00161-4>

Õppetöö:

2024 Ökoloogiliste koosluste andmeanalüüs (3 EAP), Tartu Ülikool. Loengud ja praktilise osa juhendamine.

Stipendiumid:

- 2023 Eesti doktorikooli lühiajalise mobiilsuse grant, Tartu Ülikooli Maa-
teaduste ja ökoloogia doktorikool (1500 €).
- 2022 IAVS reisistipendium, Rahvusvaheline Taimestikuökoloogia Ühing (999 €).
- 2022 DORA Pluss tegevus 1.1. – Lühiajalise mobiilsuse stipendium, Tartu
Ülikool (1240 €).
- 2019 ERASMUS-väline rahvusvahelise liikuvuse stipendium, Trieste Ülikool
(1500€).

Auhinnad:

- 2023 Noore koosluste ökoloogi auhind, parim noorteadlase ettekanne,
4. rahvusvaheline koosluste ökoloogia konverents, Trieste.
- 2022 Kolmas koht ‘2-minutilise ettekande konkurss’, EcolChange Centre of
Excellence’i lõppkonverents.
- 2022 Parim suuline ettekanne Tartu Ülikooli botaanikaosakonna doktorantide
konverentsil.

Suulised ettekanded rahvusvahelistel konverentsidel (esitav autor on alla joonitud):

Beccari, E., & Carmona, C.P. *Plant size: unifying Above and belowground dimensions*. 66th Annual Symposium of International Association for Vegetation Science. 16.–20. september 2024, Funchal, Madeira.

Tordoni, E., **Beccari, E.**, Fujinuma, J., Caleño Ruiz, B. L., Tamme, R.,
Toussaint, A., Trindade, D. P. F., Carmona, C. P. *The hitchhiker’s guide to trait imputation: empirical insights from vascular plants*. 66th Annual Symposium of International Association for Vegetation Science. 16.–20. september 2024, Funchal, Madeira.

Beccari, E., Capdevila P., Salguero-Gómez, R., & Carmona, C.P. *Mammalian life history strategies are strongly associated with environmental realms*. 11th Biennial Conference International Biogeography Society. 7.–11. jaanuar 2024, Praha, Tšehhi.

Beccari, E., Capdevila Lanzaco P., Salguero-Gómez, R., & Pérez Carmona, C. *Environment drives the position of mammalian species in the global spectrum of life histories*. 4th International Conference on Community Ecology. 20.–22. september 2023, Trieste, Itaalia.

Petruzzellis, F., Bacaro, G., **Beccari, E.**, Castello, M., Maccherini, S., Nardini, A., Pavanetto, N., Puglielli, G., Savi, T., Tomasella, M., Tonet, V., Tordoni, E. *Coordination between water-related traits and the leaf economic spectrum*. 4th International Conference on Community Ecology. 20.–22. september 2023, Trieste, Itaalia.

Beccari, E., Pérez Carmona, C., Tordoni, E., Petruzzellis, F., Martinucci, D., Casagrande, G., Pavanetto, N., Rocchini, D., D'Antraccoli, M., Ciccarelli, D. & Bacaro, G. *The devil is in the details: plant spectral diversity from high-resolution imagery captures taxonomic and functional diversity facets in coastal dune communities*. 64th Annual Symposium of International Association for Vegetation Science. 27. juuni – 1. juuli 2022, Madrid, Hispaania.

Muud teadustegevused:

Retsensent ajakirjadele Ecological Indicators [1], Ecography [1], Ecological Monograph [1], Journal of Vegetation Science [2], New Phytologist [1], OIKOS [1].

Temaatilise sessiooni korraldaja: TS(2)15. Funktsionaalse ökoloogia uued rakendused. III SIBECOL & XVII AEET kohtumine, 2.–7. juuni 2025, Pontevedra, Hispaania.

Avaldamata publikatsioon: Beccari, E. (2021). Valutazione della diversità funzionale vegetale da immagini multispettrali ad alta risoluzione: un caso studio sull'ecosistema dunale tirrenico. *Notiziario della Società Botanica Italiana* 5, lk 269.

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