

Research article

Above- and belowground traits along a stress gradient: trade-off or not?

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The role of plant traits in shaping community assembly along environmental gradients is a topic of ongoing research. It is well accepted that plant traits of aboveground organs tend to be conservative in stressful conditions. However, there is limited understanding of how belowground traits respond. Plants may have similar strategies above and belowground, but an intriguing possibility is that there is a tradeoff between above and belowground traits of communities to both ensure efficient resource-use and limit niche overlap along the gradient. To test this, we asked whether the response of above and belowground traits of communities is coordinated or not along a stress gradient in Mediterranean sand dune communities. We analyzed 80 vegetation plots in central Italy to test for coordinated vs independent patterns in above vs belowground plant traits using community weighted mean and standardized effect size of functional richness. Our results show that plant communities close to the sea, which experience higher stress, were characterized by higher convergence towards aboveground resource conservation and conservative water-use strategies but belowground resource acquisition, consistent with a strong effect of habitat filtering and an above–belowground tradeoff favoring adaptation to harsh and dry conditions. At the opposite end of the gradient with lower stress, plants exhibited higher trait diversity for both above and belowground traits, but overall a dominance of aboveground fast resource acquisition and generally acquisitive water-use strategies, combined with conservative belowground strategies. This suggests that fast growth rate aboveground was compensated by more conservative fine-root strategies, but processes such as competition limited niche overlap overall. Our findings provide new insights into the relationship between functional traits and environmental gradients in plant communities, shedding light on the tradeoffs between the above and belowground dimensions.

Keywords: belowground traits, coastal dunes, competition, habitat filtering, root traits, stress



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Introduction

Understanding the mechanisms shaping plant communities along environmental gradients is a long-standing ecological issue (Funk et al. 2017). In the last decades, researchers shed light on process contributing to community assembly by studying species' functional traits (Götzenberger et al. 2012, Funk et al. 2017, Laliberté 2017, de Bello et al. 2021, Bricca et al. 2023a). Nowadays, it is widely accepted that a local plant communities can originate from random processes such as dispersal events or priority effects or by deterministic processes operating on species niches whose relative contribution depends on the harshness of local environmental conditions (Götzenberger et al. 2012, Coyle et al. 2014, Bricca et al. 2022). For example, stressful conditions select species with largely overlapping niches that are functionally convergent (i.e. sharing more similar trait values than expected by chance) because habitat filtering processes reduce the range of successful strategies within the plant community (Weiher and Keddy 1995, Cornwell et al. 2006). On the contrary, under less stressful environmental conditions, niche partitioning processes limit the similarity of coexisting species (limiting similarity), leading to a wider range of successful strategies than expected by chance (functional divergence; MacArthur and Levins 1967). Current knowledge suggests that both random and deterministic processes can occur simultaneously, potentially affecting different sets of species traits (Carboni et al. 2014, Bricca et al. 2021).

Most investigations addressing assembly rules have focused on few aboveground traits, namely specific leaf area (SLA), plant height (H), and seed mass (SM), jointly referred to as the LHS scheme of Westoby (1998) (Laliberté 2017). These traits, collectively considered representative of the aboveground functional dimension, relate to resource exploitation (SLA), competitive ability for light (H), and reproductive ability (SM; Díaz et al. 2016). However, using only LHS traits leaves a substantial part of functional space largely unexplored, in particular the belowground dimension (Carmona et al. 2021, Klimešová and Herben 2023). Recently, belowground plant ecology research is experiencing a spiking interest, with advancements focused on fine-root traits reflecting shifts from acquisitive to conservative strategies (specific root length, SRL; root tissue density, RTD) and on belowground organ traits expressing water-use strategies (belowground organ water content, BOWC) (Freschet et al. 2010, Stanisci et al. 2010, de Bello et al. 2012, Montagnoli et al. 2012, 2014, Kramer-Walter et al. 2016, de la Riva et al. 2016, 2019, Laliberté 2017, Erktan et al. 2018, Carmona et al. 2021, Laughlin et al. 2021). These studies describe how belowground traits coordinate with aboveground ones to determine viable species ecological strategies, yet they do not provide information on community assembly mechanisms. At the same time, few efforts have been made to investigate how belowground traits contribute to plant community organization along stress gradient (Holdaway et al. 2011, Spitzer et al. 2022), and attempts

to examine aboveground and belowground plant traits in a single framework are still rare.

The simplest hypothesis is that plants may have similar strategies above and belowground, but an intriguing possibility is that there is a tradeoff between above and belowground traits of communities. For example, it has been proposed that increasing stress promotes a shift in competition from aboveground to belowground resources (Reynolds and D'antonio 1996, Coomes and Grubb 2000, Rajaniemi 2003, de Bello et al. 2012, Tilman 2020). In particular, the 'resource allocation theory' builds on the idea that under favorable conditions plant species show an aboveground acquisitive strategy by allocating relatively more carbon to aboveground (fast-growing strategies), rather than belowground organs, because of the higher competition for light (Tilman 2020). Conversely, under stressful conditions, species will shift towards belowground acquisitive strategies, limiting the aboveground biomass investment (slow-growing strategies) due to intense competition for water and soil nutrients (de Bello et al. 2012). This variation in the mode of competition might also be mirrored in opposite aboveground and belowground functional diversity patterns. In line with the limiting similarity hypothesis, we may expect that when species show a high degree of niche overlap for certain aboveground traits, the belowground functional dimensions should ensure sufficient niche partitions to allow coexistence. For example, it has been observed that along a large-scale gradient of productivity, clonal and bud bank traits diverged while LHS strategies tended to converge (Vojtkó et al. 2017). Still, opposite functional diversity patterns between aboveground and belowground ecological niche might not be the only possible coexistence solution for plants. Recently, a global investigation at the species level highlighted how LHS and fine-root traits are not aligned along the same functional axes, thus suggesting an independent contribution of these functional dimensions (Carmona et al. 2021). Nonetheless, an independence of aboveground and belowground plant traits ruling the community assembly process has never been argued before and evidence is still lacking.

In consideration of the above, this study aims at shedding light on assembly patterns of above- and belowground traits in sand dune plant communities, which are known to be highly stressful environments. Indeed, due to the presence of a steep sea-inland gradient running perpendicular to the coastline, these ecosystems feature harsh abiotic conditions, whose intensity decreases towards the inland, arguably in parallel to increasing intensity of competition (Santoro et al. 2012; Fig. 1, Supporting information). This gradient is responsible for a considerable turnover in species composition and functioning over very short distances, making coastal dunes an ideal system to test the effect of variation in stressful conditions on plant communities (Acosta et al. 2009, Carboni et al. 2011, 2016, Ciccarelli and Bona 2022). Specifically, plant communities close to the sea, which experience more stressful conditions (e.g. foredunes dominated by perennial species) are typically characterized by species with taller size and aboveground slower-growing strategies (e.g.

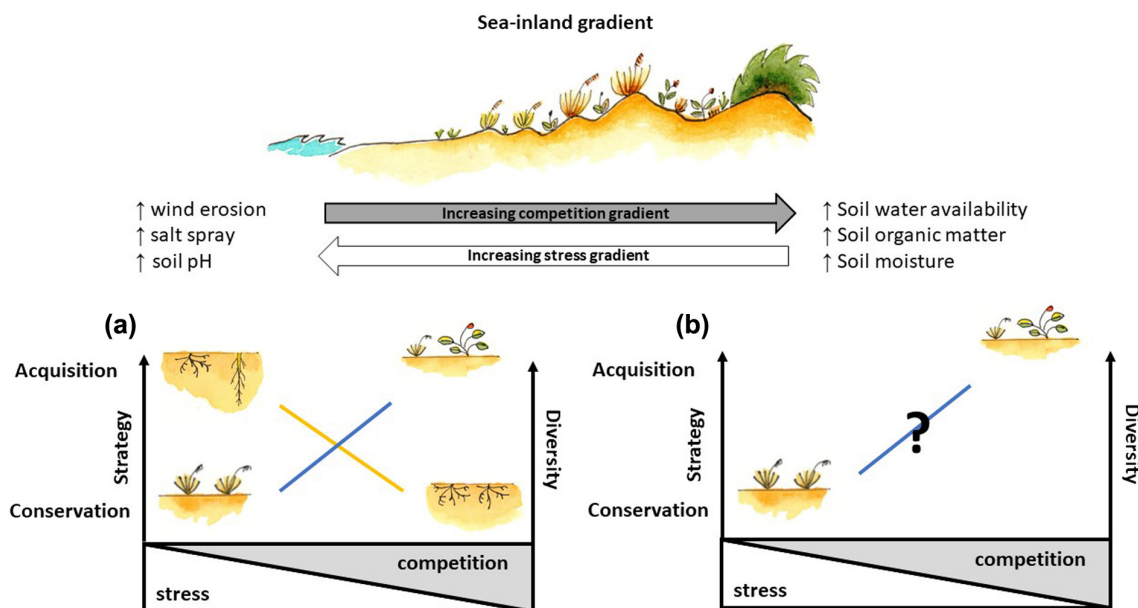


Figure 1. Conceptual framework highlighting different kinds of relationships between aboveground and belowground traits in relation to the sea-inland gradient as proxy of stress gradient; (a) according to the resource allocation theory and limiting similarity hypothesis, above- and belowground traits have opposite resource exploitation strategies (acquisition versus conservation) and trait diversity patterns; (b) alternatively, above- and belowground traits resource exploitation strategies and trait diversity are not negatively coordinated. Aboveground and belowground variation is represented by blue and orange lines, respectively. Variation of abiotic conditions along sea-inland gradient according to [Carboni et al. \(2011, Supporting information\)](#).

Calamagrostis arenaria subsp. *arundinacea* and *Thinopyrum junceum*). On the contrary, plant communities away from the sea in less stressful conditions (e.g. back dunes dominated by annual species) showed species with shorter size and aboveground faster-growing strategies (e.g. *Silene canescens*, *Festuca fasciculata*) ([Acosta et al. 2006](#), [Ricotta et al. 2012](#), [Ciccarelli 2015](#), [Carboni et al. 2016](#), [Ciccarelli and Bona 2022](#)). However, how belowground traits respond is still unknown. Thus, we selected a set of six functional traits capturing the largest amount of variation in above- (LHS) and below-ground functional dimensions (SRL, RTD, BOWC; [Carmona et al. 2021](#), [Lubbe et al. 2021](#)). We investigated if above- and below-ground traits contribute to community assembly along this stress gradient, similarly, showing opposite patterns or behaving independently. We mainly hypothesize two alternative scenarios ([Fig. 1](#)):

- 1) Patterns in aboveground traits will shift from dominance of conservative strategies (low SLA, high H, high SM) and/or functional convergence due to habitat filtering under the more stressful conditions close to the coastline, to dominance of acquisitive strategies (high SLA, low H, small SM) and/or functional divergence due to competition and limiting similarity under the milder conditions of the inland ([Fig. 1a](#)). In turn, the belowground functional pattern should shift from the dominance of acquisitive belowground traits (high SRL, low RTD, high BOWC) and/or functional divergence under stressful conditions (to compensate for high similarity in aboveground traits), to the dominance of conservative belowground strategies

(low SRL, high RTD, low BOWC) and/or functional convergence under less stressful conditions ([Fig. 1a](#));

- 2) Aboveground traits changes as in the previous scenario, whereas belowground traits are expected not to be negatively coordinated. For example, belowground traits could: 1) change similarly to aboveground traits or 2) show no variation at all due to either the constant influence of a certain driver (i.e. habitat filtering or limiting similarities) along the whole gradient or because of random processes ([Fig. 1b](#)).

Material and methods

Study area

We studied recent (Holocene) coastal dunes occupying a narrow strip (<150 m) of about 16 km length along the sea-shore of the Tyrrhenian coast of central Italy (Lazio Region). The area has a Mediterranean climate characterized by a long dry summer with low annual rainfall ([Acosta et al. 2003](#)). In coastal dunes, vegetation is generally organized along a sea-inland gradient that runs perpendicular to the coastline and gives rise to a well-known 'coastal zonation' ([Van Der Maarel 2003](#), [Acosta et al. 2007](#)). Moving away from the shoreline, upper beach communities colonizing the drift line are followed by embryonic dunes, mobile dunes and a stabilized zone dominated by herbaceous plant communities (so called 'dune grasslands'), ending up in the Mediterranean maquis ([Acosta et al. 2009](#)).

Above- and belowground traits sampling

From the ‘RanVegDunes’ database (Sperandii et al. 2017), we extracted 80 georeferenced random plots (4 m²) according to the following criteria: 1) plot classified as herbaceous habitat; 2) plot not invaded by alien species; 3) plot where aboveground traits data were available at least for those species whose relative cumulative cover reached 80% of plot total cover (separately for all the three aboveground traits; Pakeman and Quested 2007); 4) plots where aboveground traits data were available at least for two species. According to the Annex I of the Directive 92/43/EU, these plots included three different habitats: embryonic dunes (code 2110), mobile dunes (code 2120), and dune grasslands (code 2230). For each plot we obtained the distance from the sea, which has been demonstrated to be a good proxy of the sea-inland gradient, with habitats close to sea characterized by higher stress conditions (lower soil moisture and organic matter, higher pH, salt spray and wind erosion, Fig. 1, Carboni et al. 2011, Bazzichetto et al. 2016). Aboveground traits, i.e. plant height, SLA and seed mass, were extracted from ‘TraitDunes’ (TRY database no. 429; Kattge et al. 2020), a database including plant traits measured on coastal dune species in central Italy. Belowground traits were measured in the field for a total of 16 species namely dominant species for which aboveground trait data were available. Trait sampling took place in 2018, during the spring season. For each of the 16 species, we dug out 3–5 individuals using a little shovel and hands and, for each individual, we measured the water content of the main belowground organ (BOWC; %), e.g. bulb, tap root, tuber, rhizome, which is informative on water-use strategies, and two fine-root traits, i.e. specific root length (SRL; cm mg⁻¹) and root tissue density (RTD; mg cm⁻³), capturing the acquisitive and conservative strategies respectively (de Bello et al. 2012, de la Riva et al. 2019). Specifically, we collected individuals at least 10 m from each other to avoid sampling the same individuals for clonal species. Individuals collected in the field were placed in plastic bags with water and stored in a cold dark box. Once in the laboratory, individuals within plastic bags were stored in the fridge. To measure BOWC, we followed the approach of de Bello et al. (2012): within the following 24 h we cut and selected as sample the oldest parts of the main belowground organs (which in case of rhizomes correspond to the part closer to the shoot; Bricca et al. 2020), as this trait is related to resource conservation. Water-saturated samples of belowground organs were weighted and then oven-dried at 60°C for approximately 96 h, i.e. until they were completely dry. Finally, similarly to de Bello et al. (2012) we expressed the BOWC as the percentage of water content (i.e. as one minus the ratio of dry weight to fresh water-saturated weight). Although the relevance of this trait remains poorly assessed to date, its use in combination with leaf and fine-root traits is promising for understanding water use patterns (de Bello et al. 2012, Lubbe et al. 2021). Concerning fine-root traits, within the following 24 h in the laboratory we gently cleaned fine-roots with water and stored them in a 50% ethanol solution to keep them fresh for longer periods of time. Then, according

to the global protocol of trait collecting and measuring (Perez-Harguindeguy et al. 2013) fine-root samples were first scanned in a small amount of water at a resolution of 800 dpi, and then dried (at least 48 h at 60°C) and weighed. Scanned fine-roots images were processed with the WinRHIZO software (Regent Instruments). To obtain fine-roots mainly involved in absorption, we used samples with diameters less than 1 mm (De Battisti et al. 2020). Specifically, the average root diameters across all our samples were < 0.5 mm, with the only exception of *Pancratium maritimum* whose average root diameter was 2.27 mm. A description of each trait is provided in Table 1. Finally, for each species we also recorded the annual lifespan (AL) at the whole plant level as a categorical trait with values of 1 and 0 for annual versus not annual species, respectively.

Above- and belowground traits values were log₁₀-transformed before performing data analysis to improve the normality of trait distribution, except the BOWC since it was not necessary (Májeková et al. 2016).

Statistical analysis

Community analysis

To quantify variation in the functional strategies at community level, we calculated the community weighted mean (CWM; Garnier et al. 2004) for each trait separately:

$$\text{CWM} = \sum_{i=1}^S p_i x_i \quad (1)$$

where S is the number of species, p_i is the relative cover of species i ($i = 1, 2, \dots, S$), and x_i is the trait value for species i . CWMs provide complementary information to the functional diversity index, quantifying variation in the dominant functional strategies in relation to the environmental gradient. Variation of CWMs in relation to sea distance was analyzed using a fourth corner analysis (Zelený 2018). This method explores the mean trait responses to environmental gradients by simultaneously analysing the information contained in three matrices: a matrix of species composition (L, abundances of species in samples), a matrix of sample attributes (e, sea distance), and a matrix of species attributes (t, species traits). The fourth-corner approach combines all three matrices (e, t and L) by calculating the (weighted) correlation between standardized species and sample attributes using a species composition table as the weight matrix (ter Braak et al. 2018). In practice, the fourth-corner correlation cannot reach -1 or 1 unless species distributions are perfectly ordered across columns and rows (Peres-Neto et al. 2017). Together with the fourth corner we selected the row-based permutation algorithm which tests the link between plot attributes (e.g. CWM) and species composition, and it is performed by randomly shuffling plot attributes 999 times across plots. A p-value (p_r , row-based permutation) is estimated as the number ($+1$) of random squared correlations equal to or greater than the observed squared value divided by the number of permutations $+1$. By adding 1, the observed values are included as one possible value under the null distribution

Table 1. List of the aboveground and belowground traits considered, their codes (unit of measurement), their function, their expected ecological strategies in sandy dunes plant communities. Shift of trait values underlying variation in the resource strategies with increase of stress are reported with an arrow facing down if a negative relationship is expected, and facing up if a positive relationship is expected.

Functional dimension	Trait (code, unit)	Function	Resource strategies and trait states (source)	Distance to sea
Life history	Annual lifespan (AL)	Persistence	Acquisitive – annual Conservative – non annual (Perez-Harguindeguy et al. 2013)	↑
	Plant height (H, m)	Competitive ability	Conservative – high H Acquisitive – low H (Acosta et al. 2006)	↓
Aboveground	Specific leaf area (SLA, mm ² g ⁻¹)	Photosynthetic activity	Acquisitive – high SLA Conservative – low SLA (Acosta et al. 2006)	↑
	Seed mass (SM, g)	Dispersion and reproduction	Conservative – high SM Acquisitive – low SM (Carboni et al. 2016)	↓
	Specific root length (SRL, cm mg ⁻¹)	Resource acquisition	Acquisitive – high SRL Conservative – low SRL (Kramer-Walter et al. 2016)	↓
Belowground	Root tissue density (RTD, mg cm ⁻³)	Resource transport	Conservative – high RTD Acquisitive – low RTD (Kramer-Walter et al. 2016)	↑
	Belowground organ water content (BOWC, %)	Water-use	Acquisitive – high BOWC Conservative – low BOWC (Freschet et al. 2010)	↓

(Peres-Neto et al. 2017). In addition, as CWM incorporates the cover of each species, we also calculated an unweighted version of this index, the community mean (CM), using only presence/absence data. In this way we were able 1) to disentangle if community variation depends on species turnover (i.e. changes species identity across plots) or on the variation of the cover of few dominant species across plots having same species identity (de Bello et al. 2021); 2) avoid a potential mismatch for indices which combine aboveground species cover data with belowground trait values (Tsakalos et al. 2022). To analyze CMs, we used the fourth corner analysis and the same modified permutation test as for CWMs. We concluded on the presence of tradeoffs if plant communities showed contrasting aboveground and belowground strategies (e.g. acquisitive for aboveground -high SLA- and conservative for belowground- low SRL). Positive co-variation or lack of correlation between aboveground and belowground strategies were interpreted as reflecting the absence of constraints.

Patterns of community assembly for each trait were investigated with the functional richness index (Fric; sensu Villéger et al. 2008). This index has been previously linked to community assembly processes and used for detecting processes of habitat filtering and limiting similarity (e.g. driven by competition; Cornwell et al. 2006, Mason et al. 2013, Botta-Dukát and Czúcz 2016). Fric relies on the convex hull concept (i.e. the minimum convex hull which includes all species considered; Cornwell et al. 2006). Variation in Fric should reflect a variation in the range of functional strategies within the plant community, with low and high Fric pointing to, respectively, habitat filtering (niche overlapping) and limiting similarity (niche partitioning) processes in action (Cornwell et al. 2006, Mason et al. 2013). However, since Fric may increase as a

function of species richness (Mason et al. 2013), and detecting community assembly processes requires comparing observed diversity with that expected under a null model, we calculated the standardized-effect-size of Fric (SES-Fric), as follows:

$$\text{SES}(\text{Fric}) = \frac{\text{Observed Fric} - \text{Mean Expected Fric}}{\text{SD Expected Fric}} \quad (2)$$

When SES-Fric < 0, the observed functional richness in a community is lower than expected by chance ('functional convergence' or 'niche overlapping'). Instead, when SES-Fric > 0, the observed functional richness is higher than expected by chance ('functional divergence' or 'niche partitioning'). We calculated expected Fric values by shuffling trait values across all species within the dataset 999 times. This algorithm is equally sensitive to functional convergence due to habitat filtering as well as to functional divergence due to limiting similarity processes (Botta-Dukát and Czúcz 2016). To assess the variation of functional patterns along the sea-inland stress gradient, for each trait we computed Pearson's coefficient correlation between the SES-Fric values and sea distance. As for CWMs, we concluded on the presence of a trade-off (limiting similarity processes acting between the aboveground and belowground functional traits) if e.g. in plant communities aboveground strategies converged (SES-Fric < 0) and belowground traits diverged (SES-Fric > 0). Positive co-variation or its absence represents evidence for independence, as this would indicate that assembly of species via aboveground traits is not constrained by belowground functional patterns.

All analyses were run in the R environment (ver. 4.1.2, www.r-project.org). Functional richness (Fric), CWM and CM

were calculated with the *dbFD* function in the 'FD' package (Laliberté et al. 2014), while the fourth corner analysis was run with *test fourth* function in the 'weimea' package (Zelený 2020).

Results

Regarding the variation in the functional strategies (CWM), we found significant and positive co-variation with distance to the sea for SLA (corr=0.18; Fig. 2c) and BOWC (corr=0.14; Fig. 2f) and significant negative co-variation for SRL (corr= -0.19; Fig. 2e). Moreover, we found co-variation close to significant for the SM (corr=-0.13; Fig. 2c) and mostly a lack of co-variation for both H (corr=-0.12; Fig. 2a) and RTD (corr=0.06; Fig. 2d). Similar patterns resulted also from the unweighted version of this index (i.e. community mean, CM), with the only exception of the negative co-variation of H and SM which became significant (Supporting information).

Concerning community assembly patterns (SES-Fric), we found a significant variation in the range of functional strategies (SES-Fric) along the sea-inland environmental

gradient for all the considered traits (Fig. 3). There was a similar positive trend of all the traits with sea distance, ranging from a convergence pattern (SES-Fric < 0) in plant communities closer to the sea, to a divergence pattern (SES-Fric > 0) in more inland plant communities. The strongest positive correlation resulted for the aboveground traits of SLA and SM (corr=0.31 and corr=0.39, respectively; Fig. 3b–c) and for the belowground traits SRL and BOWC (corr=0.36 and corr=0.32, respectively; Fig. 3e–f).

Discussion

In this study we found that plant trait variation followed partly predictions from the resource allocation theory but was also partly independent for above and belowground traits, depending on which aspect of community organization was involved. Specifically, the variation in the functional strategies (CWM or CM) confirmed our first scenario, i.e. the presence of a tradeoff in the resource allocation between aboveground and belowground organs (Tilman 2020). Plant communities growing in stressful conditions (i.e. close to the seashore) were characterized

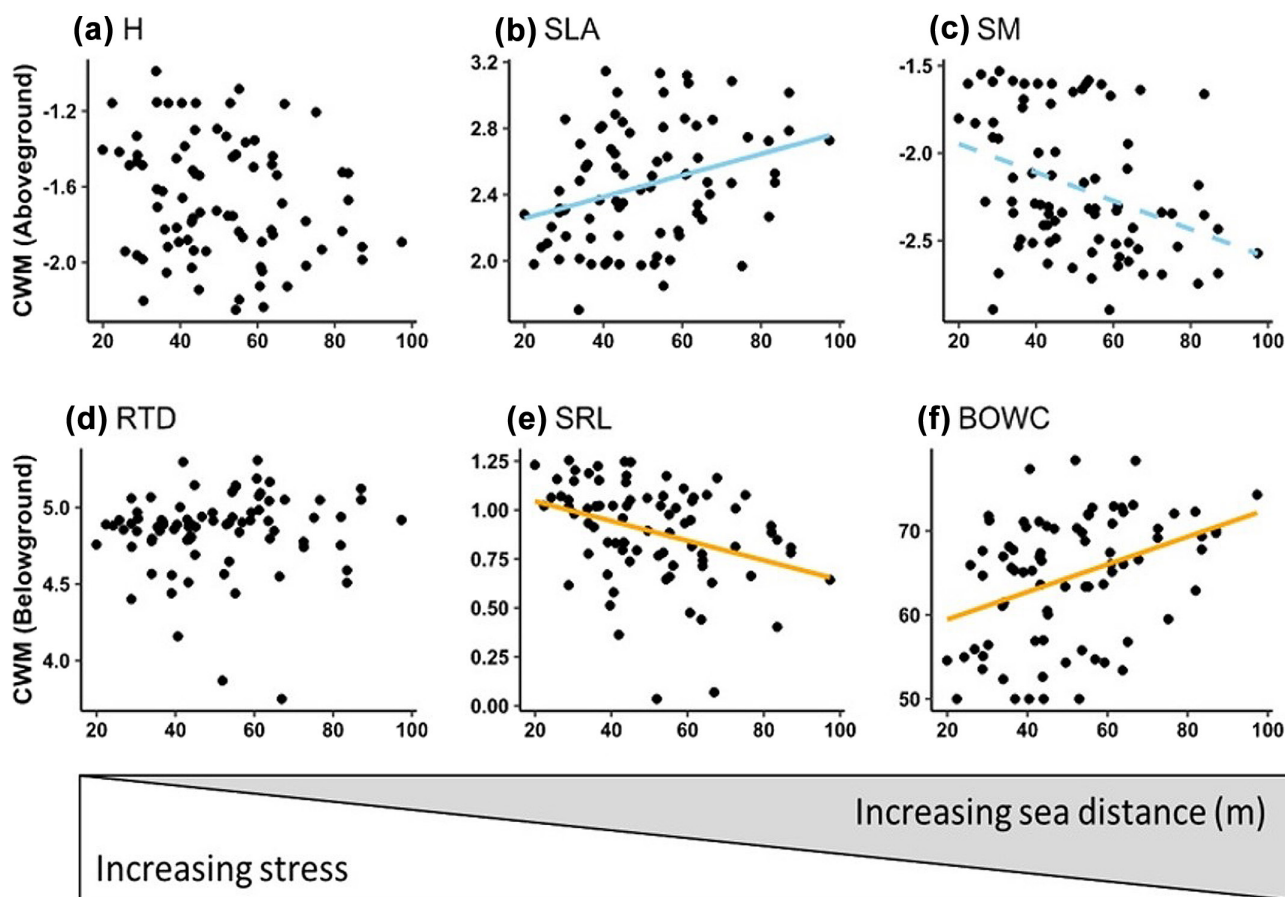


Figure 2. Co-variation of community weighted mean (CWM) in relation to sea distance (m) for aboveground traits: (a) plant height (H, m), (b) specific leaf area (SLA, $\text{mm}^2 \text{g}^{-1}$), (c) seed mass (SM, g), and belowground traits: (d) root tissue density (RTD, mg cm^{-3}), (e) specific root length (SRL, cm mg^{-1}), (f) belowground organ water content (BOWC, %). Significant co-variations ($p < 0.05$) are represented by a solid skyblue and orange line for aboveground and belowground traits, respectively. Close to significant co-variation ($p < 0.10$) are represented by dotted line. All the selected traits, excepted for BOWC, were \log_{10} -transformed before calculating the CWM.

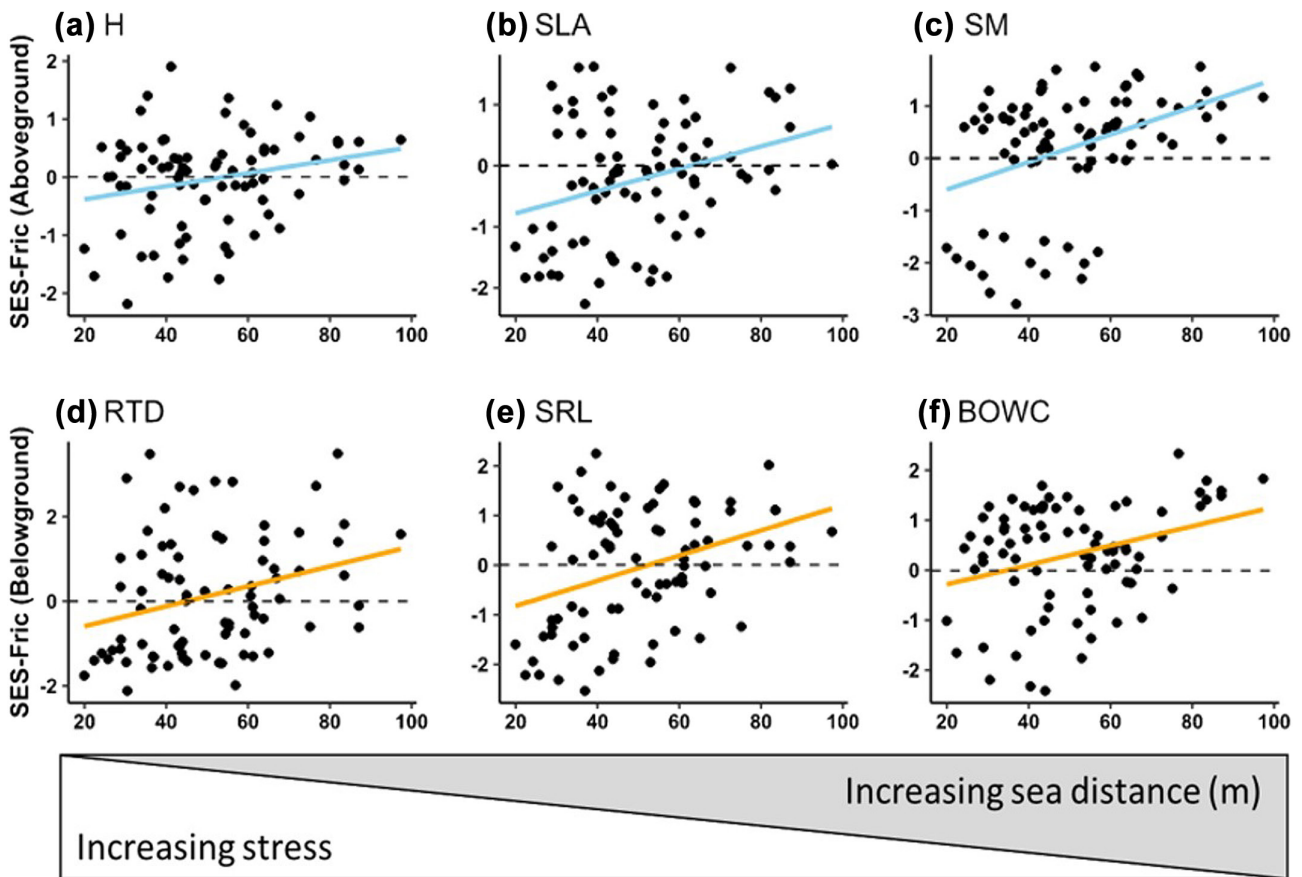


Figure 3. Co-variation of standardized effect size of functional richness (SES-Fric) in relation to sea distance (m) for aboveground traits: (a) plant height (H, m), (b) specific leaf area (SLA, $\text{mm}^2 \text{g}^{-1}$), (c) seed mass (SM, g), and belowground traits: (d) root tissue density (RTD, mg cm^{-3}), (e) specific root length (SRL, cm mg^{-1}), (f) belowground organ water content (BOWC, %). Significant co-variations ($p < 0.05$) are represented by a solid skyblue and orange line for aboveground and belowground traits, respectively. All the selected traits, excepted for BOWC, were \log_{10} -transformed before calculating the SES-Fric.

mainly by aboveground conservative strategies (low SLA) coupled with conservative water strategies (low BOWC) but with acquisitive fine-root strategies (high SRL). At the opposite end of the gradient, in less stressful conditions (i.e. far from the shoreline), plant communities showed high photosynthetic rate (high SLA) coupled with less conservative water-use (high BOWC) but high conservative fine-root strategies (low SRL) (Fig. 4a). In terms of assembly rules (SES-Fric), the results were in line with the second scenario, in which aboveground and belowground traits contribute independently to community assembly. Higher stress conditions promote functional convergence for all selected traits, probably driven by habitat filtering processes, while under lower stress conditions, functional divergence dominates for both above and belowground traits, consistently with strong limiting similarity processes, potentially related to more competitive interactions (Fig. 4b).

Dominant strategies (CWM): resource allocation theory

Our observed variation in functional strategies supported Tilman's hypothesis (2020), that plant species occurring in

resource-rich environments should show acquisitive strategies mainly for aboveground organs, while belowground acquisitive strategies should be favored under stressful conditions. In our study, plant communities closer to the sea (foredunes) are subject to high stress (incoherent and unfertile soils, wind erosion, aridity and salinity) where water and soil nutrients represent the main limiting resource (Carboni et al. 2011). These conditions favor persistence of plant communities dominated mainly by taller species with long lifespan (Supporting information) like *C. arundinacea* and *T. junceum*, displaying overall aboveground conservative strategies complemented by water-conservative strategies (low SLA and low BOWC) (Stanisci et al. 2010). Indeed, species growing in drought conditions tend to use water more efficiently (Freschet et al. 2010, de Bello et al. 2012). Moreover, this environmental severity is also well reflected by the acquisitive pattern we found for fine-roots. In line with studies finding an increase of SRL in response to nutrient limitation and water availability, we found species growing closer to the sea are characterized by high SRL values (Zangaro et al. 2008, Holdaway et al. 2011, Kramer-Walter et al. 2016, De Battisti et al. 2020). High SRL is associated with enhanced

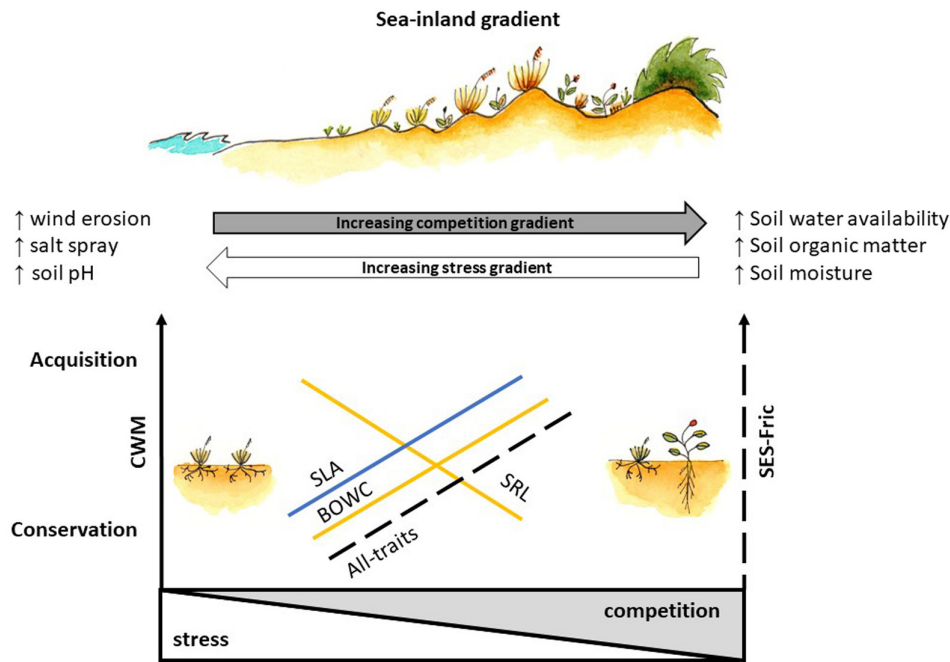


Figure 4. Conceptual illustration of the results showing different patterns in aboveground and belowground traits in relation to the sea-inland gradient as a proxy of a stress gradient. Our results indicate that functional dominant strategies (CWM) changed as predicted by the resource allocation theory with an increase towards stressful conditions of aboveground conservative (low SLA) and water-saving strategies (low BOWC) coupled with belowground acquisitive strategies (high SRL). However, all the selected traits showed an independent contribution (H, plant height; SLA, specific leaf area; SM, seed mass; SRL, specific root length; RTD, root tissue density; BOWC, belowground organ water content) to community assembly (SES-Fric) since they are all filtered by stressful conditions.

root proliferation and the production of thinner and lighter fine-roots, which in nutrient-poor environments represents an effective strategy to promote nutrient acquisition by exploring higher soil volume per unit carbon investment in root length (Laliberté et al. 2015).

Moving away from the sea (dune grasslands), the functional portfolio of plant communities shifts completely. Here, where stress relaxes and resource availability increases, plant communities showed aboveground acquisitive strategies (high SLA) coupled with less conservative water-use strategies (high BOWC). This pattern is perfectly in line with the trends we found belowground for SRL, which was lower in grasslands far from the sea with more coherent and nutrient-rich soils. Indeed, it has been suggested that under fertile soils thicker root cortex (i.e. low SRL) supports higher metabolic rates (Chimungu et al. 2014, Kramer-Walter et al. 2016). This functional portfolio of plant communities far away from the sea can be also ascribed to the increase of annual species compared to foredunes (Supporting information). Generally, annual species have shorter lifespans, investing most of the energy in fast growth (high SLA and SRL) and in considerable seed production, resulting in less conservative water-use (high BOWC) (Supporting information). However, contrary to what reported in the literature (Roumet et al. 2006), here we found annual species with lower SRL compared to non annual ones (Supporting information), probably as a consequence of a lower root proliferation in the soil. These shifts in the dominant functional strategies were confirmed

and emerged even more clearly when considering presence/absence species data (CM, Supporting information). Variation in CWMs could result just from changes in the cover of few dominant species, while variation in CM exclusively depends on species turnover (de Bello et al. 2021), confirming that the considerable turnover in species composition due to the sea-inland gradient also reflects in a clear functional turnover (Acosta et al. 2003). Finally, we should note that in our case, weighting belowground traits with aboveground species cover or using the unweighted version of the index, produce consistent results. However, we cannot exclude that incorporating abundances measured belowground could produce different results, calling for further investigation (Tsakalos et al. 2022).

Community assembly patterns (SES-Fric): independent contribution

The existence of tradeoffs between functional dimension in community assembly processes is a fascinating idea, yet only partially supported by evidence (Lhotsky et al. 2016, Vojtkó et al. 2017). Given that the overlap of species niches within a community is limited, it is expected that if some traits converge, others should diverge and that this opposite pattern should be stronger in case of traits capturing similar functions for different functional dimension (i.e. SLA for aboveground and SRL for belowground) (MacArthur and Levins 1967, Lhotsky et al. 2016, Vojtkó et al. 2017). However, our study challenges the generality of this tradeoff, at least in terms of

LHS aboveground traits vs. belowground organ and fine-root traits. We found significant variation for all traits towards the same direction (i.e. functional convergence under higher stress conditions), independently of whether these were above or belowground traits. The functional convergence can be ascribed to the effect of habitat filtering, as only specialized species are able to persist in such harsh ecological conditions (Ricotta et al. 2012, Carboni et al. 2016).

While functional convergence for aboveground traits confirms previous results from these environments (Ricotta et al. 2012, Carboni et al. 2016), the belowground functional pattern does not support the presence of above–belowground tradeoff. Therefore, an interesting question arises: how can species coexist in the stressful conditions close to the sea-shore if they are functionally similar both in their aboveground and belowground traits? One possible explanation is that traits may have diverse competitive outcomes affecting mechanisms of species coexistence. For example, belowground traits like SRL and BOWC should connect to size-symmetric competition (Rajaniemi 2003, Mayfield and Levine 2010), meaning that small differences in competitive ability do not have disproportionate effects on competitive exclusion. Thus, species with similar niches are more likely to coexist (Rajaniemi 2003). Additionally, selective pressure for niche differentiation between co-existing species should be less intense in stressed communities and fitness should be guaranteed by traits that maximize acquisition and retention of limiting belowground resources (Holdaway et al. 2011, Mason et al. 2013).

In contrast, other traits like plant height are related to size-asymmetric competition, which means that a small difference in plant size may promote strong competitive exclusion (Rajaniemi 2003). Taller species displace shorter ones and the resulting plant community is composed only by dominant species displaying similar size (Lepš 2014). However, plant communities close to the sea are characterized by scattered vegetation with very low cover, suggesting that competitive exclusion is not a key community assembly driver (Santoro et al. 2012).

At the opposite end of the gradient, i.e. far away from the sea, the presence of higher resource availability promotes functional divergence for all considered traits. Our finding supports the idea that resource-rich communities have greater functional diversity than resource-poor communities both above and belowground (Mouchet et al. 2010, Mason et al. 2013). This functional pattern is consistent with strong limiting similarity, a hypothesis suggesting that species that are quite different can assemble even under strong competition because they exploit different niches (Stubbs and Wilson 2004, Carboni et al. 2016). Such higher diversity is also consistent with the presence of species having completely different life-histories, including annual (e.g. *S. canescens*, *F. fasciculata*) and non-annual species (e.g. *Lotus cytisoides*, *Plantago macrorrhiza*) (Supporting information). Indeed, a functional divergence is expected when species belonging to different life lifespan coexist together (Gross et al. 2013, Klimešová and Herben 2023).

Conclusion

Coastal dunes are very peculiar ecosystems characterized by a strong sea-inland gradient of stress which determines a trade-off in resource allocation between above- and belowground organs. Nonetheless, belowground traits assembled independently of aboveground traits, providing poor support for the idea that limiting similarity results in the differentiation of belowground traits to compensate for functional convergence of aboveground traits. Close to the sea, low nutrient and water availability limits the number of species able to survive and filters species with a stress-tolerant strategy, i.e. mostly perennial species with water-saving strategies and acquisitive root system aimed at a better soil exploration of the limiting water/nutrient resource. Along the gradient, moving away from the sea stress, the increase in nutrients and soil moisture allows more diverse species to survive by partitioning the available niche space. As stress conditions relax, we observed the coexistence of both stress-avoidance (i.e. annual species) and stress-tolerant strategies (i.e. perennial species), displaying overall higher aboveground acquisitive strategies but conservative fine-root traits. We are aware that other functional dimensions can play a role in promoting species coexistence like phenology, however the selected traits probably represent those explaining higher variation in the plant functional spectrum. Our study reinforces the viewpoint that community organization is more complex than expected and, more importantly, that the exclusive use of aboveground traits provides only a partial picture of plant communities.

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Alessandro Bricca: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Marta G. Sperandii:** Formal analysis (supporting); Writing – review and editing (supporting). **Alicia T. R. Acosta:** Data curation (lead); Visualization (supporting); Writing – review and editing (supporting). **Antonio Montagnoli:** Conceptualization (supporting); Methodology (supporting); Software (supporting); Writing

– review and editing (supporting). **Greta La Bella:** Writing – review and editing (supporting). **Mattia Terzaghi:** Software (lead). **Marta Carboni:** Conceptualization (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/doi:10.5061/dryad.d51c5b07r> (Bricca et al. 2023b).

Supporting information

The Supporting information associated with this article is available with the online version.

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