An integrated phenotypic trait-network in thermo-Mediterranean vegetation describing alternative, coexisting resource-use strategies

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HIGHLIGHTS

- Inter and intra-specific phenotypic variation stabilises ecosystem function.
- We studied phenotypic integration patterns in thermo-Mediterranean vegetation.
- And found a spectrum of alternative, coexisting, resource-use strategies
- Phenotypic plasticity aided complementarity among functionally distinctive species.
- And defined the breadth of species' climatic niches

GRAPHICAL ABSTRACT

ARTICLE INFO

ABSTRACT

Vascular plants have been found to align along globally-recognised resource-allocation trade-offs among specific functional traits. Genetic constrains and environmental pressures limit the spectrum of viable resource-use strategies employed by plant species. While conspecific plants have often been described as identical, intraspecific variation facilitates species coexistence and evolutionary potential. This study attempts to link an individual's phenotype to its environmental tolerance and ecosystem function. We hypothesised that: (1) seasonal variation in water availability has selected for tight phenotypic integration patterns that shape Mediterranean vegetation; however, (2) coexisting species employ alternative resource-use strategies to avoid competitive exclusion; specifically (3) species with smaller climatic niches (i.e. potential distributions) display higher functional diversity. We examined the interdependence among and the sources of variation within 11 functional traits, reflecting whole-plant economics (e.g. construction costs, hydraulics, defences, water storage capacity), from nine dominant, thermo-Mediterranean species measured across a wide environmental and geographic gradient. Furthermore, we delineated the phenotypic and climatic hypervolumes of each studied species to test for climatic niche overlap and functional distinctiveness. By adopting this multidimensional trait-based approach we detected fundamental phenotypic integration patterns that define thermo-Mediterranean species regardless of life history strategy. The studied traits emerged intercorrelated shaping a resource-allocation spectrum. Significant intraspecific variability in most measured traits allowed for functional distinctiveness among the measured species. Higher functional diversity was observed in species restricted within narrower climatic niches. Our

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results support our initial hypotheses. The studied functional traits collectively formed an integrated space of viable phenotypic expressions; however, phenotypic plasticity enables functionally distinctive species to succeed complementary in a given set of environmental conditions. Functional variability among coexisting individuals defined species' climatic niches within the trait-spectrum permitted by Mediterranean conditions. Ultimately, a species establishment in a locality depends on the extent that it can shift its trait values.

1. Introduction

Phenotypic variation in physiological traits among coexisting individuals was the key observation that laid the foundation for the theory of evolution (Darwin and Wallace, 1858). Through natural selection organisms develop adaptations, which grant them advantages against the pressures they face into their habitats. This way the observed phenotypic inter- and intra-specific variation translates into functional diversity. But not all probable phenotypes demonstrate equal fitness. Genetic constrains and environmental pressures outline the spectrum of viable resource-use strategies employed by plant species.

A species' resource-use strategy defines its competitive ability, and thus its successful establishment in a community (Reich et al., 2003; Grime, 2006). Global covariation patterns among specific functional traits, measured across spatial and taxonomic scales, define fundamental resource-allocation trade-offs (i.e. economics spectra) that are systematically used to describe global trends in phenotypic variation along environmental gradients, determine species' distributions, and comprehend the spectrum of plants' productivity and performance (Reich et al., 2003; Wright et al., 2004; Grime, 2006; Díaz et al., 2016). Plant species have been found to align along continuous spectra of economically-viable investment designs; for example the leaf economics spectrum (LES, Wright et al., 2004) that extends from species with inexpensive, ephemeral leaves (i.e. rapid returns on carbon and nutrient investments), to the more conservative ones carrying well-protected tissues.

Díaz et al. (2016) demonstrated that vascular plants occupy only a fraction of the potential phenotypic space that would exist if no limitations were posed on individuals. Since the prolific genetic variation does not appear to be the main limiting factor, phenotypic selection on combinations of traits must be adaptive (Donovan et al., 2011). Phenotypic integration patterns (i.e. covariation among functionally related traits in a given organism) can be viewed both as (genetic/biochemical) constraints, which limit evolutionary trajectories, and as adaptations to environmental filtering (Pigliucci, 2003). Life history theory predicts the existence of a whole-plant strategy, with plant traits merged into a single axis of variation representing the spectrum of viable resource-investment designs (Brodribb, 2009; Reich, 2014; Díaz et al., 2016). Since resource allocation patterns act at the individual level, they must result in analogous construction costs among organs; however, empirical studies from different systems show contrasting evidence. Ultimately, trait relationships should depend on whether integration (see for example Freschet et al., 2010; Méndez-Alonzo et al., 2012; Pérez-Ramos et al., 2012; Messier et al., 2017, studying resource-limited systems) or interdependence (see for example Wright et al., 2007; Fortunel et al., 2012; Kramer-Walter et al. 2016) of functionally related traits is favoured under given environmental pressures. Abiotic stressors have been found to act as macro-environmental filters, driving plant strategy selection (Pérez-Ramos et al., 2012; Le Bagousse-Pinguet et al., 2017). Water-stressed communities for example tend to be dominated by conservative species with higher tissue dry matter content and water-use efficiency (Grime, 2006; Pérez-Ramos et al., 2012). However, within the range permitted by climatic constrains alternative, viable resource-use strategies can coexist (Gross et al., 2013; Le Bagousse-Pinguet et al., 2017).

Biotic interactions (i.e. competition and facilitation) modify the local abiotic environment thus limiting the functional similarity of coexisting species (Macarthur and Levins, 1967). Niche differentiation allows species to minimize spatially and temporally their resource-requirement overlaps, and reduces interspecific competition in a given habitat (Pacala and Tilman, 1994; Ashton et al., 2010; Maire et al., 2012). According to the productivity hypothesis, functional diversity is expected to decrease in stressful environments due to stronger abiotic filtering (de la Riva et al., 2017; Schellenberger Costa et al., 2017). However, niche complementarity, spatial micro-heterogeneity and positive interactions have been found to facilitate the coexistence of multiple life strategies towards the limiting end of gradients by increasing overall resource utilization (Pacala and Tilman, 1994; Maire et al., 2012; Gross et al., 2013; Ratcliffe et al., 2016). The stabilising role of phenotypic variation in ecosystem function has been argued extensively in ecology, yet most studies focus on species diversity, omitting biologically relevant variability among the individuals of a species. While conspecific plants have often been described as identical, intraspecific variation allows individuals of a species to survive, grow, and reproduce under varied environmental conditions by influencing their responses to habitat and community changes (Clark, 2010; Violle et al., 2012). A species' niche can be delineated as a hypervolume defined by the multidimensional, Euclidean space of its ecological variables (e.g. functional traits or abiotic tolerances) within which it can maintain a viable population (Hutchinson, 1957). Since ecosystem function ultimately depends on species' traits in a community, exploring to what extent local factors affect them can advance our understanding of how climate change and other anthropogenic drivers will alter ecosystem services (Bruelheide et al., 2018).

We draw attention to the southern European Mediterranean ecosystems because increased summer water-limitation and extreme drought events are predicted for the region (Spinoni et al., 2018), while 36 to 69% of the plant species they host are expected to perish by 2080 with global mean temperature increase of 2 to 4.5 °C respectively (Warren et al., 2018). Variation in water-availability has been identified as one of the predominant factors limiting plant establishment (Engelbrecht et al., 2007) and carbon cycling (van der Molen et al., 2011). However, even under similar environmental conditions, plant communities can vary greatly in their species' traits. The high habitat heterogeneity that characterizes these systems, declares Mediterranean ecosystems excellent sites for studying environmental constraints on species' traits. Observed warming and drying trends along with land-use changes, habitat-fragmentation, and intense human pressures (i.e. over 10 millennia of continuous human settlement) restrict further natural adaptation responses, painting an uncertain picture for the current vegetation of the region (Choat et al., 2012).

This paper aims to offer insights into the interdependence among and the sources of variation within 11 plant functional traits and how individuals from nine, dominant, lowland, thermo-Mediterranean species with contrasting life history strategies optimise them to succeed in their local environments along Greece. We constructed a large, systematic traits database reflecting whole-plant economics (e.g. construction costs, hydraulics, defences, water storage capacity) across a range of environmental conditions. We estimate functional redundancy and climatic niche overlap by delineating the phenotypic and climatic spaces of the studied species, with the n-dimensional niche space method (Blonder et al., 2018) based on the Hutchinson's multidimensional niche concept (Hutchinson, 1957). We hypothesised that: (1) seasonal variation in water availability has selected for tight phenotypic integration patterns that shape Mediterranean species regardless of

life history strategy; however, (2) coexisting species with dissimilar growth forms and leaf life-spans that experience strong resource-competition employ alternative resource-use strategies to avoid competitive exclusion; more specifically (3) species with smaller climatic niches (and thus potential distributions) display higher functional diversity.

2. Material and methods

2.1. Study location and species

The topographic configuration of Greece, defined by significant elevation shifts, produces a considerable variety of climate types within relatively short distances. Extended mountain ranges stretch across the continental country from North to South, creating rain-shadow affected areas at the East and more humid regions to the West and North. Lower-elevation hilly provinces are characterized by Mediterranean-type climate with mild, wet winters and warm, dry summers (di Castri, 1981), while temperate climate occurs at higher elevations along the northern border of the country (Yassoglou et al., 2017).

This study focuses on thermo-Mediterranean vegetation: the dominant, lowland, vegetation type of Greece (over 40% of the country's surface, Arianoutsou and Diamantopoulos, 1985) and the Mediterranean Basin; consisting of both evergreen arborescent and seasonal-dimorphic shrubs, and coniferous trees. We studied nine, characteristic of the Greek landscape, and widespread throughout the Mediterranean Basin, species across their distribution in Greece: strawberry tree *Arbutus unedo* and Greek strawberry tree *Arbutus andrachne* (broadleaved evergreen arborescent shrubs), a mock privet species *Phillyrea latifolia*, lentisc *Pistacia lentiscus*, and kermes oak *Quercus coccifera* (all sclerophyllous evergreen arborescent shrubs), two rock-rose species *Cistus salviifolius* and *Cistus creticus* (short seasonal-dimorphic shrubs), and Aleppo *Pinus halepensis* and Anatolian pine *Pinus brutia* (two native thermo-Mediterranean coniferous trees that cover extended areas in the lower elevations of the Mediterranean Basin and their distributions meet in Greece).

2.2. Sampling design

This study was designed to follow the nine, selected species across a range of environmental conditions throughout Greece. Field campaigns took place from 2012 to 2015 always during the growing season (i.e. April to July), which was tracked according to elevation, aspect, and field observations, as to sample the individuals of a given species at a similar phenological stage (i.e. before the seasonal-dimorphic *Cistus* shrubs shed their winter foliage: summer leaves are not productive, but rather act as triggers for winter leaves, Arianoutsou and Diamantopoulos, 1985). To reduce variation further, we only sampled sunlit, fully-mature (but not senescing) leaves. Each sampling site was selected to contain at least five, distinct individuals of as many species of interest as possible, while at the same time being satisfactorily uniform (e.g. vegetation composition, aspect, elevation), so that differences between sites assimilate environmental heterogeneity. We selected an adequate number of contrasting sampling areas for each species (65 unique sampling sites: on average 19 per species), as to capture the widest possible climatic heterogeneity of their distribution, in an attempt to cover the full natural range of their trait values along Greece (Fig. S1). We accomplished a latitudinal range from 35.05 to 41.23°N, a longitudinal range from 20.47 to 26.60°E, and an elevational range from 2 to 1298 m above sea level, mean annual temperature (T_{mean}^{an}) ranged from 9.3 to 18.6 °C, while total annual precipitation ($Prec^{an}$) ranged from 445 to 1176 mm, among our sampling sites (Table S1).

2.3. Functional traits

Eleven functional traits, directly or indirectly associated with resource-economics at organ, individual, and ecosystem scale, were measured:

- SLA (specific leaf area, $m^2\,kg^{-1}$: the projected area of a fresh leaf, or a needle, by its oven-dry mass) represents the light-capturing foliar area per unit of invested leaf biomass: and as such regulates leaf maximum photosynthetic rate, whole-plant potential growth-rate, and ecosystem productivity (Reich et al., 1997; Wright et al., 2004).
- LDMC (leaf dry matter content, $mg\,g^{-1}$: the oven-dried mass of a leaf, or a needle, by its water-saturated mass) reflects the balance between mesophyll and structural compounds (Garnier and Laurent, 1994): thus affects directly leaf function, defence, whole-plant metabolism, aboveground primary productivity (Wilson et al., 1999), as well as decomposition rate, and (through that) soil fertility (Kazakou et al., 2009).
- L_{Th} (leaf thickness, mm: of a leaf's lamina measured between veins, or a needle) determines physical strength, and controls CO_2 diffusion rates, and thus photosynthetic capacity, growth rate, and resource-use strategy (Witkowski and Lamont, 1991).
- LNC and LPC (leaf nitrogen and phosphorus concentrations, both in $mg\,g^{-1}$: the total amount of N and P per unit of leaf dry mass) follow closely each other, and define leaves' chemical defence and decomposability, thus driving biogeochemical cycles; their patterns affect directly light harvesting and gas fluxes, hence photosynthetic potential; while their restricted availabilities control growth rate and carbon acquisition (Reich et al., 1997; Wright et al., 2004).
- LCC (leaf carbon content, $mg\,g^{-1}$: the total amount of C per unit of leaf dry mass) effectively describes a trade-off between hydraulic and mechanical efficiency on leaf architecture (Niinemets et al., 2007).
- L_A (the projected leaf area, cm^2), while a component of SLA, represents an independent axis of variation among species (Ackerly et al., 2002). L_A, L_W (leaf width), and L_L (leaf length) regulate leaf energy and water balance (Valladares and Niinemets, 2007). Relationships among architectural traits, broadly observed across environments and phylogeny, describe alternative adaptive designs in response to biophysical constraints (Niinemets et al., 2007; Díaz et al., 2016).
- $L_A{:}B_A$ (the leaf area to basal area ratio, $m^2\,m^{-2}$: the total L_A that a stem of certain diameter carries) expresses a trade-off between mechanical support and transport functions: driven via plant biomechanics and metabolic scaling (i.e. retaining a constant carbon assimilation rate per unit crown area) (Enquist and Niklas, 2002), aims to minimize leaf overlap, and thus maximize photosynthesis (Sack and Holbrook, 2006).
- SWD (stem wood density, $g\,cm^{-3}$: the oven-dried mass of a section of a terminal branch by its volume) expresses the biomass invested in solid material (e.g. cell wall, parenchyma) versus void (e.g. lumen of fibres, tracheids, conductive elements), thus directly associated with construction costs it reflects a trade-off between growth and survival potential (Brodribb, 2009). High-density wood (compiled by small cells with thick walls and limited intercellular space) offers hydraulic efficiency and resistance to mechanical damage and pathogen attack: thus enhanced lifespan but slower growth (Enquist et al., 1999; Jacobsen et al., 2007; Chave et al., 2009).

2.4. Functional traits measurements

Widely accepted field and lab protocols, and quality control procedures were applied (Cornelissen et al., 2003). We randomly selected five, sexually mature, healthy, unshaded individuals from each species within each sampling site (810 unique individuals: on average 90 per species). Approximately 0.5 kg of healthy, terminal branches, from around the crown, were collected from each individual and stored in

paper bags. As soon as possible after sampling, three terminal branches per individual, with all their leaves still attached, were placed in water and left in the dark to saturate. After at least 10 h, the total number of leaves in each branch and its diameter were recorded, so the average $L_A:B_A$ per individual could be calculated. 5 leaves, or 10 needles, from each branch, were selected to capture the variability within individuals. After removing the petiole (and the rachis in *P. lentiscus*), we measured the average L_{Th}, L_L, L_W and saturated weight of the 15 leaves, or compound leaves, or 30 needles per individual, before scanning them to calculate their area (ImageJ, NHI, version 1.47). Furthermore, we recorded the dry weight of the leaves, after oven drying them for 48 h at 60 °C, to calculate SLA and LDMC. A finely-ground sample of dried leaves per individual (0.1 g) was analyzed for the estimation of LNC and LCC, using a LECO elemental analyzer (TruSpec Micro, St. Joseph, USA) according to manufacturer's instructions. An additional finely-ground sample of dried leaves per individual (0.2 g) was microwave-digested in HNO_3/H_2O_2 mixture, and LPC was determined via the colorimetric ascorbic acid method (EPA, 1978). Finally, we recorded the volume, utilizing the Euclidean method (i.e. water-replacement), and weight of a branch section per individual, after oven drying it for 48 h at 60 °C, to calculate SWD.

2.5. Statistical analysis

To establish phenotypic integration we examined the interdependence of the measured functional traits. First we tested for significant, bivariate relationships using Spearman's correlation for every trait pair, and standardised major axis regressions (SMA) in all statistically significant occasions. SMA regression is deemed appropriate since there is no clear dependent or independent variable, but rather an interest in the slope between each pair. Moreover, we performed network analysis (igraph R package, Csardi and Nepusz, 2006) to graphically represent the coordination among the measured traits in Mediterranean, thermophilous vegetation. We generated an undirected network with traits as nodes and the significant correlations among them as edges. For reproducibility the edge list was shorted from the most powerful correlation to the least. Each trait's position in the correlation network was optimised by the Kamada-Kawai algorithm that attempts to minimize the energy in a spring system (Kamada and Kawai, 1989). The algorithm creates a virtual dynamic system in which every two nodes are connected by a "*spring*". In the initial structure the length of each "*spring*" matches the correlation strength between the two traits. Then the algorithm draws the optimal layout by producing symmetrical graphs with relatively small number of edge crossings, such that the position of each trait, relative to the rest, reflects the correlation strengths of the whole network. Community structure among traits was tested via greedy optimisation of modularity. Nodes' degree centrality (i.e. number of adjacent edges) was calculated (as an indicator of network's centrality) to identify the most important (i.e. highly-connected) traits in the phenotype. To test whether these trade-offs hold regardless of life history strategy we divided our dataset in four subsets: "*broadleaved evergreen arborescent shrubs*", "*sclerophyllous evergreen arborescent shrubs*", "*seasonal-dimorphic shrubs*", and "*coniferous trees*" and repeated the analyses for each subset.

Furthermore, traits' covariation in the multidimensional space was estimated via principal components analysis (FactoMineR R package, Lê and Husson 2008), performed on the standardised full dataset with "*species*", "*life history strategy*", and "*site*" as supplementary, categorical variables. Principal components (PCs) with eigenvalues lower than one were disregarded as insignificant, and the cross-correlation matrix between the active, continuous variables (i.e. traits), the supplementary, categorical variables (i.e. "*species*", "*life-history-strategy*", and "*site*") and the remaining PCs was calculated. The supplementary variables were not involved in the construction of the PCs, thus their correlation reveals the relative position of each species, life history strategy, and site on the multidimensional plane.

To describe functional diversity we looked for within traits variation. First, we examined each trait's dispersion in the full dataset and among the individuals of each species and life history strategy, and searched for statistically significant differences between the different species and life history strategies, and across sampling sites (Kruskal-Wallis one-way analyses of variance, R Core Team, 2017). Furthermore, nested random effects models (lme4 R package, Bates et al., 2015) were fitted in the following syntax: Trait ~ (1|Genus/Species/Site) + (1|Site), to partition each trait's variance among components expressing: variation between genera, species, within-species variability (i.e. variation among individuals of a species within a site), and environmental acclimation (i.e. variation among sites). All factors were treated as random without interaction term, and all parameters were estimated by the restricted maximum likelihood method. Visual inspection of the residual plots did not reveal any obvious deviations from homoscedasticity or normality, so we proceeded with variance components analysis. Each factor's significance was inferred with parametric bootstrapping. All traits' values (apart from L_{Th}, LPC and LCC) were Box-Cox transformed prior to fitting the models. The proposed model syntax is biologically realistic since it allows individuals of different species to occur across a variety of habitats, and enables us to study variation among them, as well as along environmental gradients.

Moreover, we estimated the occupied phenotypic and climatic spaces of the studied species in Greece. For each of the nine species we constructed a 9-dimensional, phenotypic hypervolume from its measured, standardised, trait values, excluding SLA and L_W. Highly correlated dimensions produce degenerated results; to avoid that, from the two trait-pairs with |r| > 0.7 in our dataset (SLA–LDMC and L_A–L_W) we chose to exclude the traits exhibiting the lowest degree centrality in the full network. Additionally, we obtained four bioclimatic variables: T^{an}_{mean}, $Prec^{an}$, and mean temperature and precipitation of the warmest quarter (Bioclim variables 1, 12, 10 and 18), from the WorldClim database (Fick and Hijmans, 2017), at 30 second spatial resolution (~1 km), for the Greek territory (34.8–42°N and 19.5–28.5°E). We standardised each variable, and extracted climate values for each species-plot combination in our dataset, in order to infer each species' 4-dimensional, climatic niche in Greece. Seasonal precipitation was included since it is known to control tree growth regardless of annual availability (Fyllas et al., 2017). All hypervolumes were constructed using Gaussian kernel density estimation (hypervolume package, Blonder et al., 2018), with probability quantile 0.95, and Silverman bandwidth estimator. Dimensionality was validated by assessing each variable's contribution to the total hypervolume, as the ratio of the original n-dimensional hypervolume, relative to each of the possible, n − 1 dimensional hypervolumes produced by removing each variable. The structure of our dataset permits us to employ this non-parametric approach that allows for irregular trait distributions, incorporates the multidimensional nature of the phenotypic and climatic spaces across scales, considers intraspecific variation, and shows sensitivity to gaps in hypervolumes. We estimated species' functional redundancy and climatic niche overlap by calculating Sørensen similarity index (i.e. the intersection of a pair of hypervolumes, by their mean volume) for each species' pair. Finally, we tested the relationship between species' phenotypic and climatic spaces with SMA regression.

3. Results

3.1. Phenotypic integration in thermo-Mediterranean vegetation

We detected 29 fundamental bivariate, allometric relationships that define thermo-Mediterranean vegetation regardless of life history strategy (Fig. S2, Table S2). SLA scaled negatively with LDMC, L_{Th} and SWD and positively with LNC, LPC, L_A and L_W, while the reverse was true for LDMC. LNC and LPC covaried, while both scaled negatively with L_{Th} and SWD in most cases. Architectural traits (i.e. L_A, L_W, L_L, and $L_A:B_A$) emerged highly interlinked, and negatively associated with L_{Th} (across

all life strategies but coniferous trees) and LCC (across all life strategies but seasonal-dimorphic shrubs). The graphical representations of traits coordination in Mediterranean, thermophilous vegetation and among the alternative life history strategies revealed integrated phenotypic networks with high edge densities (i.e. proportion of present edges from all possible edges in the network) and low modularities (Fig. 1), suggesting coordinated phenotypic responses.

When we partitioned the phenotypic covariation structure into distinct components three axes explained 72% of the total inertia (Fig. 2, Table S3). The first principal component (PC, 32%), strongly influenced by structural traits (i.e. SLA, LDMC and nutrient concentrations), opposed conservative individuals (with high LDMC, LCC, L_{Th}, and SWD), characterized by a strong positive coordination to the axis, to individuals with larger, lighter and nutrient-richer leaves (with high SLA, LNC and LPC) (i.e. the seasonal-dimorphic *Cistus* shrubs in our dataset, from which winter leaves were sampled). The second PC (27%), highly correlated with architectural traits, discriminated the broadleaved evergreen arborescent *Arbutus* shrubs, against species with alternative leaf strategies. But these two axes alone did not expose the full picture: the third PC (14%) was positively driven by L_{Th} and L_L, and negatively by SWD; and along this axis we were able to distinguish among the conservative resource-use strategies, employed by the sclerophyllous evergreen arborescent shrubs and coniferous trees considered in this study.

3.2. Sources of phenotypic variation

In the dataset presented here, with the exception of the rather stable LCC and SWD, measured traits exhibited significant dispersion (Table S4). Statistically significant differences among and between the different species and life history strategies, and across sampling sites were detected for all traits (analyses of variance, Fig. 3 & Table S3).

The majority of variance in most foliar traits was attributed to interspecific differences (i.e. "*Genus*" and "*Species*" components: L_W 94%, L_L 78%, L_A 73%, LCC 71%, LDMC 59%, L_{Th} 56%, L_A:B_A 53%) (Fig. 4). Nevertheless, almost all measured traits displayed considerable within-species (up to 15% for LNC and L_{Th}) and among sites (up to 40% for SLA, 36% for LPC, 24% for LNC and SWD, and 20% for L_{Th}) variation. SLA (intra 46%, inter 43%), LPC (intra 46%, inter 27%), LNC (intra 38%, inter 32%), L_{Th} (intra 34%, inter 56%) and SWD (intra 34, inter 26%) in particular emerged almost equally affected by inter and intra-specific pressures (i.e. "*Site*" and "*Individual*" components).

### 3.3. Climatic niche overlap and functional distinctiveness

For each of the studied species we delineated its 9-dimensional, phenotypic (from its measured traits values) and 4-dimensional, climatic (inferred by mapping occurrence data to climatic data) spaces in Greece (Fig. 5a; Table S5). Sørensen similarity indices were calculated to test whether co-occurring species employ alternative resource-use strategies (Fig. 5b). We found high overlap (>60% in most cases) among the climatic niches of the measured species, with the exceptions of *C. salvifolius*, *P. halepensis*, and *P. lentiscus*, which appeared to occupy unique, climatic spaces that they shared in some degree. In contrast, all species, even closely-related ones, emerged functionally distinctive (5–14% functional overlap among species' pairs). Furthermore, we observed that as a rule, species with smaller climatic niches displayed higher functional diversity (Fig. 5c).
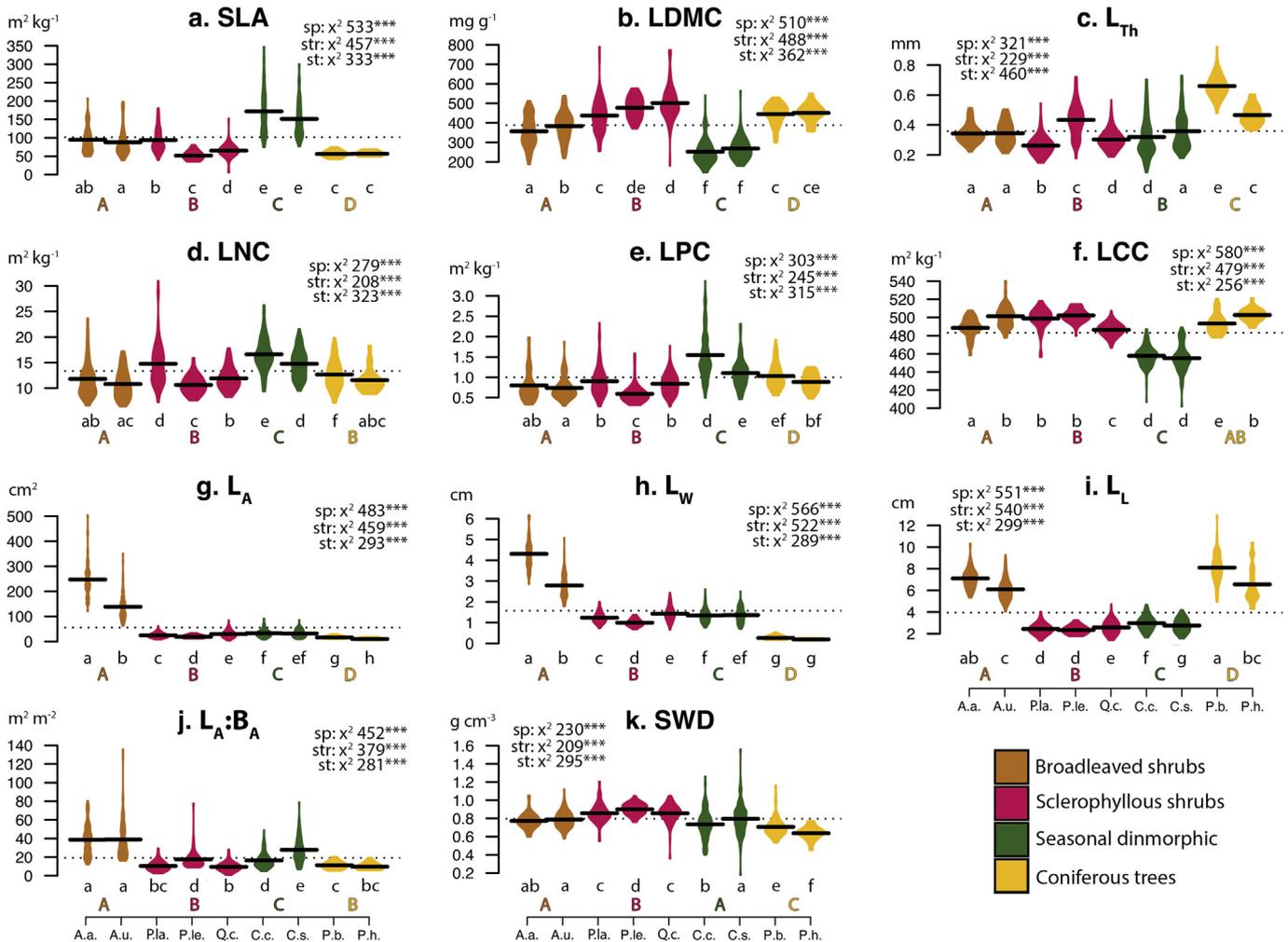
4. Discussion

In this study we found a highly integrated (i.e. edge density 76%) phenotypic trait-network in thermo-Mediterranean vegetation
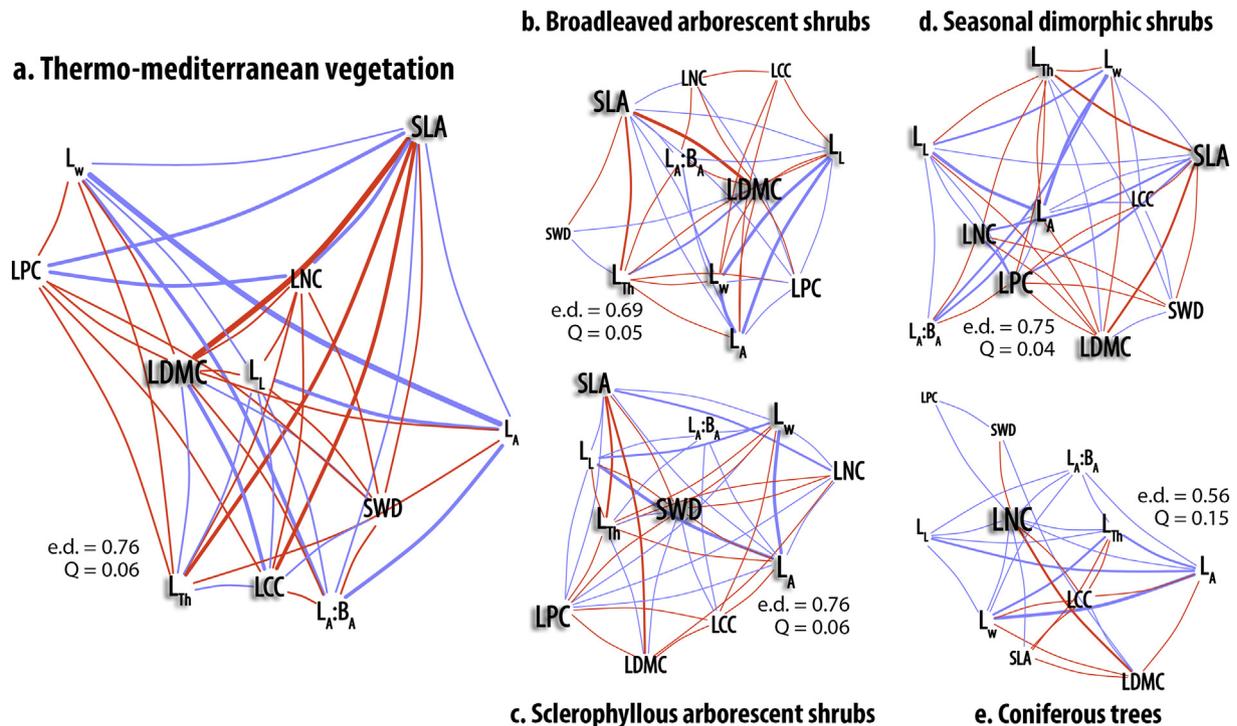

Fig. 1. Traits' correlation networks graphically represent in a two-dimensional plane the coordination among the 11 functional traits, measured in Mediterranean, lowland, thermophilous vegetation along Greece (a) for the full dataset and (b through e) among alternative life history strategies. Traits' position in the networks was optimised by the Kamada-Kawai algorithm to reflect the correlation strengths of the whole network (e.d., edge density: the proportion of present edges from all possible edges in each network; Q, modularity). Blue lines indicate positive correlations and red negative (see also Fig. S2), thin lines are used for |Spearman's r| < 0.50, intermediate when 0.51 < |r| < 0.80, and thick lines for |r| > 0.81. Label size expresses traits' degree centrality (i.e. number of adjacent edges); labels with shadows indicate the most connected (i.e. with >8 out of 10 possible significant correlations) traits in each network (SLA, m² kg⁻¹: specific leaf area; LDMC, mg g⁻¹: leaf dry matter content; L_{Th}, mm: leaf thickness; LNC, LPC & LCC, mg g⁻¹: leaf nitrogen, phosphorus & carbon concentrations; L_A, cm²: leaf area; L_W, cm: leaf width; L_L, cm: leaf length; L_A:B_A, m² m⁻²: leaf area-basal area ratio; SWD, g cm⁻³: stem wood density). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
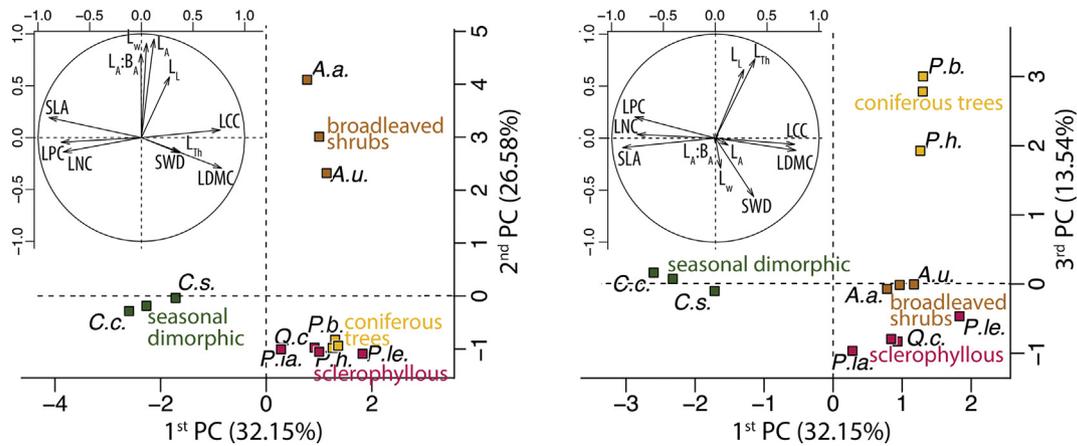
Fig. 2. Traits contribution and species and life history strategies relative position along the first three principal components (PC) produced by an analysis performed on 11 functional traits, measured in Mediterranean, lowland, thermophilous vegetation along Greece, with "species" and "*life-history-strategy*" as supplementary, categorical variables (see also Table S3). Colours signify the alternative life histories of the studied species (n = 810; SLA, m² kg⁻¹: specific leaf area; LDMC, mg g⁻¹: leaf dry matter content; L_{Th}, mm: leaf thickness; LNC, LPC & LCC, mg g⁻¹: leaf nitrogen, phosphorus & carbon concentrations; L_A, cm²: leaf area; L_W, cm: leaf width; L_L, cm: leaf length; $L_A:B_A$, m² m⁻²: leaf area-basal area ratio; SWD, g cm⁻³: stem wood density; A.a.: *Arbutus andrachne*; A.u.: *Arbutus unedo*; C.c.: *Cistus creticus*; C.s.: *Cistus salviifolius*; P.b.: *Pinus brutia*; P.h.: *Pinus halepensis*; P.la.: *Phillyrea latifolia*; P.le.: *Pistacia lentiscus*; Q.c.: *Quercus coccifera*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)


Fig. 3. Traits' Kernel distribution density aggregated at species level, along with the results of the Kruskal-Wallis one-way analysis of variance (***: p < 0.001) among the different species (sp), life history strategies (str), and sampling sites (st, see Fig. S1) for 11 functional traits, measured in Mediterranean, lowland, thermophilous vegetation along Greece (see also Table S4). Under each trait the results of the Conover's post hoc test for each species (black) and life history strategy (coloured) are given. Black dashes represent the mean (n = 810; SLA: specific leaf area; LDMC: leaf dry matter content; L_{Th}: leaf thickness; LNC, LPC & LCC: leaf nitrogen, phosphorus & carbon concentrations; L_A: leaf area; L_W: leaf width; L_L: leaf length; $L_A:B_A$: leaf area-basal area ratio; SWD: stem wood density; A.a.: *Arbutus andrachne*; A.u.: *Arbutus unedo*; C.c.: *Cistus creticus*; C.s.: *Cistus salviifolius*; P.b.: *Pinus brutia*; P.h.: *Pinus halepensis*; P.la.: *Phillyrea latifolia*; P.le.: *Pistacia lentiscus*; Q.c.: *Quercus coccifera*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
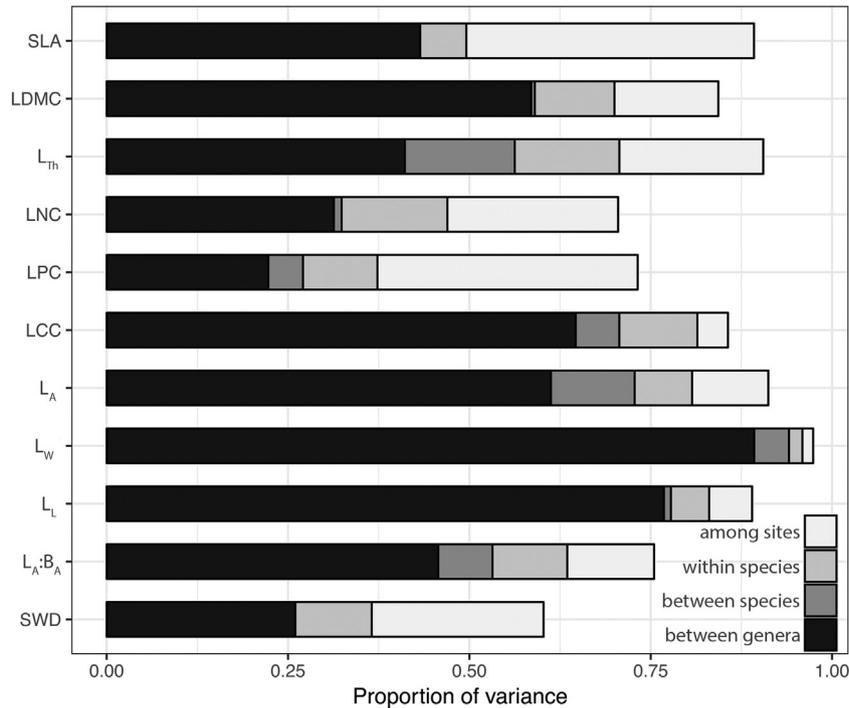
Fig. 4. Variance partitioning for each of the 11 functional traits, measured in Mediterranean, lowland, thermophilous vegetation along Greece, among the interspecific (between genera and between species) and intraspecific (within species and among sampling sites) components. Factor significance was inferred with parametric bootstrapping and all factors in all models were highly significant (p < 0.001; n = 810; SLA, m^2 kg^{-1}: specific leaf area; LDMC, mg g^{-1}: leaf dry matter content; L_{Th}, mm: leaf thickness; LNC, LPC & LCC, mg g^{-1}: leaf nitrogen, phosphorus & carbon concentrations; L_A, cm^2: leaf area; L_W, cm: leaf width; L_L, cm: leaf length; L_A:B_A, m^2 m^{-2}: leaf area-basal area ratio; SWD, g cm^{-3}: stem wood density).

(Fig. 1a) describing alternative resource-use strategies coexisting along Greece (Figs. 2 & 5b). The studied traits emerged intercorrelated (Fig. S2a, Table S2a) revealing a coordinated trait space of plant form and function (Fig. 1a). We report fundamental phenotypic integration patterns that extent beyond the traits traditionally considered in the LES, and shape thermo-Mediterranean species regardless of growth form and leaf habit (Figs. 1b–e & S2b–e, Table S2b–e). Mediterranean conditions dictate for integrated plant evolution in tissue construction
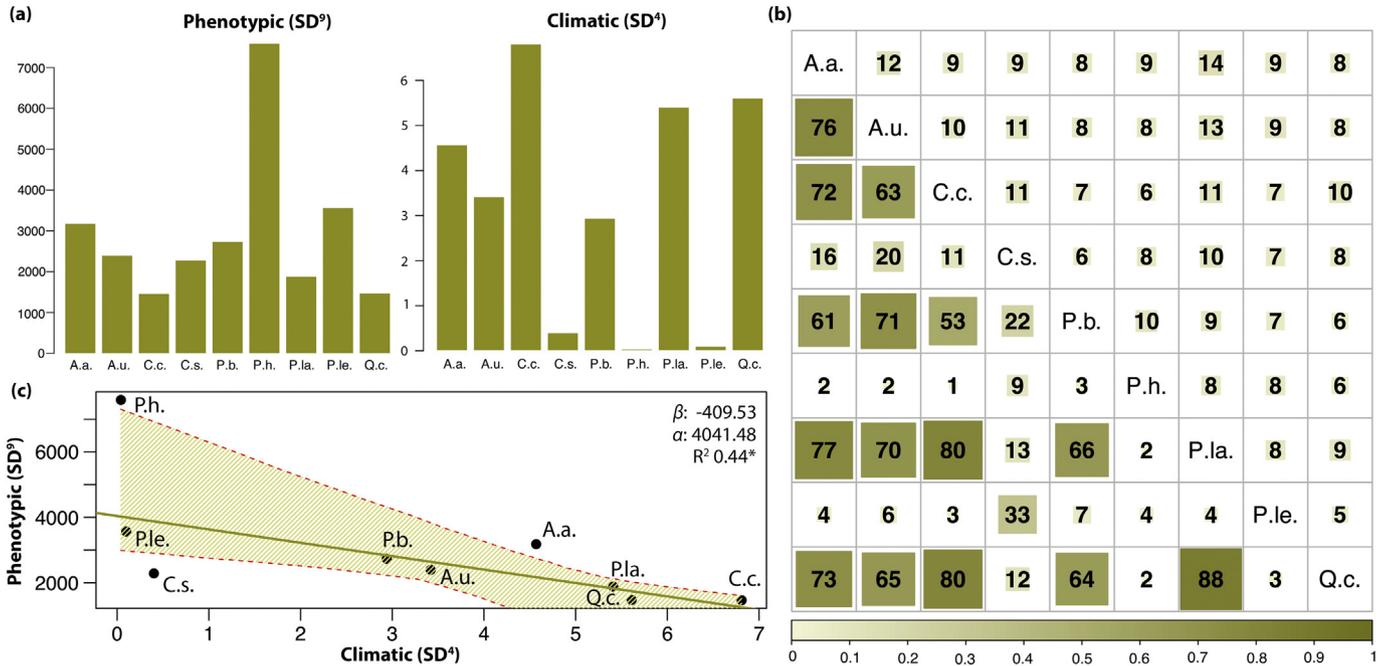
Fig. 5. a. Species phenotypic, 9-dimensional (constructed by species' measured, trait values) and climatic, 4-dimensional (inferred by mapping species occurrence data to climatic data) hypervolumes' volumes (in units of standard deviations (SD) to the power of the number of dimensions) (see also Table S5). b. Climatic (below the diagonal) and phenotypic (above) hypervolumes' overlaps for each species' pair (note that Sørensen similarity index coefficients are translated into percentages) c. Species' phenotypic and climatic hypervolumes fitted with a standardised major axis regression line, the polygon between red lines shows the 95% confidence interval inferred via bootstrapping (*: p < 0.05; Spearman r: −0.85, p > 0.005) (A.a.: *Arbutus andrachne*; A.u.: *Arbutus unedo*; C.c.: *Cistus creticus*; C.s.: *Cistus salviifolius*; P.b.: *Pinus brutia*; P.h.: *Pinus halepensis*; P.la.: *Phillyrea latifolia*; P.le.: *Pistacia lentiscus*; Q.c.: *Quercus coccifera*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in order to cope with increased needs for summer transpiration and cavitation risk and balance between mechanical-support, water-conductance, and storage (Vilagrosa et al., 2012; Lopez-Iglesias et al., 2014). Our results compliment recent studies conducted in rangelands of southern France (Pérez-Ramos et al., 2012) and forests and shrublands of southern Spain (de la Riva et al., 2016) affirming the existence of an integrated, whole-plant survival strategy in Mediterranean vegetation. Functional integration could be proven pivotal in tying phenotypic variation with environmental tolerance and ecosystem function.

These relationships expose a resource-allocation trade-off, from fast-growing, acquisitive tissues with higher nutrient concentrations, to thick and sturdy leaves and stems providing hydraulic efficiency (Fig. 2, Table S3). Díaz et al. (2016), at the species level (based on 2214 species), and Bruelheide et al. (2018), at the community level (based on 1.1 million plots), report the same global functional continua, suggesting that species-level trade-offs constrain community assembly despite the fact that species with opposing trait values can coexist within the same community (Bruelheide et al., 2018). Niche complementarity and environmental filtering are defined by local interactions at the individual level and sessile organisms have been found to modify their traits in response to the activity of their closest neighbours (Miller et al., 2007).

An individuals' position in this functional space was determined by its morphology and function. The studied species employ alternative, integrated survival strategies (Figs. 2 & 3, Table S3). The resource-acquisitive strategy (i.e. high SLA and nutrient concentrations, and low LCC, LDMC, and SWD) was employed by seasonal-dimorphic shrubs during the favourable months (i.e. autumn to spring). But high use of resources (carbon, nutrients, and water) that leads to rapid acquisition and growth is not a competitive strategy during the limiting period (i.e. summer) (Grime, 2006). Seasonal dimorphism is an adaptation to summer drought that produces seasonal different phenotypes from the same individual. Indeed, both studied *Cistus* species undergo extensive foliage replacement in order to survive drought before the dry and hot summer. Alternatively, resource conservation enhances survival by allowing plants to avoid or tolerate harsh conditions while at the same time control resource-availability to levels competitors cannot endure (Vilagrosa et al., 2012). We noticed that individuals forming thick (with high LDMC), needle-shaped leaves to avoid dehydration also composed conductive stems (i.e. low SWD), which can increase water uptake. Mediterranean pines reduce drastically water-loss by stomatal closure, and cease growth during drought, but maintain the ability to recover fast when conditions become favourable (Borghetti et al., 1998; Martinez-Ferri et al., 2000). On the other hand, evergreen arborescent shrubs were located towards the conservative extreme of the resource-allocation spectrum by showing high stem wood density, leading to expensive stem construction costs, but at the same time high hydraulic efficiency. Reduced water supply to the leaves induces lower photosynthetic and hence growth rates, yet higher tolerance to drought and thus survival rates (Grime, 2006; Chave et al., 2009). Sclerophyllous evergreen arborescent shrubs carry long-lived, tough, fibrous leaves characterized by efficient resource conservation, with low SLA, LNC, and LPC and high LDMC, and LCC (i.e. the sclerophylly syndrome). This suite of correlated traits describes a survival strategy adapted to minimize nutrient loss and increase competitive ability in dry and unproductive habitats by favouring resource allocation to storage and defences (Wright et al., 2004; Grime, 2006; Pérez-Ramos et al., 2012). Broadleaved evergreen arborescent shrubs managed to maintain larger photosynthetic area (higher L_A, L_W, L_L, and $L_A:B_A$) by forming more conductive stems (lower SWD) than sclerophyllous species.

Phenotypic variation is created by traits' variability in response to a range of ecological and evolutionary mechanisms, and can have genetic and environmental sources since most traits exhibit intermediate heritability (Bolnick et al., 2011). However, different mechanisms act at different scales so by partitioning a trait's total variance we can estimate the relative effect sizes of different drivers of phenotypic variation (Messier et al., 2017). Most variation was observed at the interspecific level for many of the studied foliar traits, especially the leaf size traits (L_W: 94%, L_L: 78%, and L_A: 73%), indicating that an individuals' phenotype is predominantly driven by species evolutionary histories and taxonomy (Fig. 4). Plant optimisation models postulate that organ-level traits will vary mostly at the interspecific level as opposed to whole-plant traits that display higher intraspecific variation attributed to genetic drivers (i.e. genetic drift, mutations, gene flow, natural selection) and local environmental factors (Siefert et al., 2015). Despite the fact that we only studied organ-level traits, we still found that for all traits a non-negligible amount of variation was attributed to differences among conspecific individuals (~15%) and sampling sites (~40%). Phenotypic plasticity (i.e. facultative character displacement) allows a given genotype to produce different phenotypes in response to local environmental conditions and enables populations to persist under new, even sub-optimal, conditions thus allowing time for new genetic variation to arise, so natural selection can increase the fit to these conditions (Pigliucci, 2005). High phenotypic plasticity facilitates coexistence and resource partitioning (Clark, 2010), particularly for species demonstrating highly overlapping resource-use patterns (Ashton et al., 2010).

Given that each species has a considerable, but (genetically constrained and thus) finite, degree of variability in its phenotypic expression, environmental filters acting on trait values determine species' survival strategies and distributions in nature. The studied species shared highly overlapping climatic niches and demonstrated high functional distinctiveness supporting our second hypothesis for character-displacement (Fig. 5b). This functional distinctiveness suggests that a species establishment in a locality depends on the extent that it can shift its trait values. Niche differentiation among coexisting species averts competitive exclusion by promoting complementary use of limiting resources (Pacala and Tilman, 1994; Gross et al., 2007; de la Riva et al., 2017). We observed a pattern whereas species with broader climatic niches (and thus potential distribution) displayed smaller phenotypic spaces, while higher phenotypic variability was manifested by species restricted in narrower climatic niches (Fig. 5c). Environmental severity has been found to stimulate functional dissimilarity (Maire et al., 2012; Ratcliffe et al., 2016) which can benefit co-occurring species under high recourse-competition conditions by reducing interspecific competition, thus promoting long-term species coexistence (Clark, 2010). Studying Mediterranean woody communities established along a drought gradient de la Riva et al. (2018) reported larger leaf phenotypic spaces on drier habitats, supporting growth forms with alternative resource-uptake and drought-survival strategies (e.g. evergreen and seasonal-dimorphic shrubs), as opposed to wetter communities that exhibited higher species-similarity.

In this paper we present a large, systematic record of 11 plant functional traits (Fig. 3, Table S4). The studied traits collectively formed a spectrum of viable phenotypic expressions; however, according to alternative designs hypothesis, different trait combinations can produce equivalent fitness in a given set of environmental conditions, and allow the co-occurrence of functionally distinctive species (Gross et al., 2013; Le Bagousse-Pinguet et al., 2017). We worked across a regional scale, covering large spatial extent and environmental heterogeneity, to provide our database with appropriate ecological breadth (Fig. S1, Table S1). We considered intraspecific variation among mature leaves in the same phenological stage along temperature and moisture gradients, and found it to translate to alternative, coexisting resource-use strategies among the studied co-occurring species. Our analysis demonstrates the adaptive effect of intraspecific variation on the observed trait space and we concur with other scholars that it contributes significantly to total trait variation, even if it generally concedes to interspecific (Jung et al., 2014; Siefert et al., 2015). Considering traits as mean values per species disregards the evolutionary history of a species, i.e. its ability to utilize resources and endure others (Ashton et al., 2010), and

ultimately misrepresents the degree of niche and trait overlap between species (Hoffmann and Merilä, 1999).

5. Conclusions

Plant functional traits directly or indirectly involved in the resource acquisition-conservation trade-off emerged integrated into a phenotypic network in thermo-Mediterranean vegetation regardless of life history strategy (Fig. 1). Our results support our first hypothesis and concur with empirical evidence from a variety of systems reporting tight phenotypic integration patterns for the regulation of water-flux (e.g. Méndez-Alonzo et al., 2012; Lopez-Iglesias et al., 2014). Carbon economics imply that the net carbon gain of an organism over its lifetime must be greater than its investment, thus it is physically impossible to maximize both durability and productivity. We report a spectrum of alternative, coexisting strategies for resource exploitation in thermo-Mediterranean vegetation (Figs. 2 & 3), driven by natural selection within the limits of biophysical constraints posed by species life-histories, and we emphasise the influence of local environmental drivers on functional traits' variation at local scales (especially SLA, leaf nutrient concentrations and thickness and stem wood density, Fig. 4). Our results suggest that functional variability among coexisting individuals defines species' climatic niches within the trait-spectrum permitted by Mediterranean conditions (Fig. 5). Our study highlights the role of phenotypic diversity in facilitating functionally distinctive species to succeed complementary along Greece. We believe that consideration of intraspecific variability has the potential to expand our understanding of the evolutionary importance of traits.

Conflict of interest

The authors declare that they have no conflict of interest.

CRediT authorship contribution statement

Chrysanthi Michelaki: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration. **Nikolaos M. Fyllas:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing - review & editing, Supervision. **Alexandros Galanidis:** Investigation, Writing - review & editing. **Maria Aloupi:** Validation, Investigation, Resources, Writing - review & editing. **Eleftherios Evangelou:** Investigation, Resources, Writing - review & editing. **Margarita Arianoutsou:** Conceptualization, Resources, Writing - review & editing, Supervision. **Panayiotis G. Dimitrakopoulos:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.04.030.

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