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Mediterranean Forests in Transition (MEDIT): Deliverable No8

Title: Report on optimum PFTs definition

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Summary

This document reports on the numerical techniques applied to define plant functional types (PFTs) for Mediterranean forests. The analysis presented here uses data gathered at the leaf, individual and stand level. The key assumption is that the way suites of functional characters coordinate can reveal life history strategies, that are associated with the local environmental conditions. In order to avoid an "*a-priory*" PFTs definition based on taxonomy (this analysis has been made in deliverable 7) we use a multivariate technique to define the PFTs based on their trait values. The outputs of this technique are then compared with the a classic taxonomy-based definition. By defining these new PFTs we provide to the vegetation modelling community a set of Mediterranean PFTs with parameter (traits) estimates that can be readily used when simulating forest dynamics following the classic approach of representing diversity with PFT, i.e. the first-generation of vegetation dynamics models. In an ecological perspective we validate to what extent taxonomy can be used to categorize species in terms of their structure and function. All analyses were made with the R programming language (R Development Core Team, 2015).

Introduction

Given the diversity of plant form and function ecologist have struggled to find ways to systematically categorise different plant taxa. The classic way of doing that is through taxonomy (Stace 1991). An alternative way which has also been widely used in modelling is by grouping species to Plant Functional Types (Box 1996, Lavorel et al. 1997). PFTs are groups of species that present a similar response to given environmental conditions or have the same effect on ecosystem processes (Lavorel and Garnier 2002). Most vegetation dynamics models are using PFTs definitions that are based on life form and general taxonomic descriptions, for example conifer trees or evergreen broadleaved shrubs (Sitch et al. 2003).

During the last decade a wealth of functional traits data have been gathered for various ecosystems around the world (Kattge et al. 2011), and this has enabled the use of various numerical techniques aiming at defining PFTs based on "first principles" (Condit et al. 1996, Pilar and Sosinski 2003, Fyllas et al. 2012). Here we follow the same route and use a multivariate approach to optimally define PFTs.

Materials and Methods

Our analysis is based on the application of Principal Components Analysis on species traits tables and the subsequent clustering of the species scores to numerically define PFTs. Three trait tables have been used with increasing level of trait information. The first table is using the leaf structural and chemical data measured in MEDIT. The second one includes leaf fluxes, such as saturated photosynthetic rate and dark respiration. The third table includes data on species specific maximum height and seed mass.

Filling the Traits Table

In order to create the table that provides the best estimate of species characteristics, we used results from various analyses and database. The leaf structural, chemical and gas exchange data were extracted from the mixed effect models described in Deliverable 7 (D5.1). Wood density values were also extracted from this analysis. The species specific traits values used here are the REML estimates of the traits genetic component i.e. when the environmental variation has been removed and species are considered to be found at a "neutral" environment.

The traits table was enhanced with additional traits from our field measurements and from our literature review. These characters include:

a) Maximum Tree Height (Hmax). Taller plants have the advantage of harvesting more light during their life time compared with shorter ones (Poorter et al. 2005) and reduce light availability of their smalle competitors. On the other hand smaller stature species tend to be more shade tolerant and present higher survival rates.

b) Seed Mass. Seed mass is generally considered to trade-off with seed number, with species of small seed size presenting higher fecundity and large seeded species being more tolerant under shade or drought conditions (Muller-Landau 2010).

Maximum Height

Species specific maximum height was estimated using the height vs diameter at breast height measurements from the MEDIT dataset. We used non linear regression models (nls2 package) to fit the following equation:

$$H = H_{\max} \cdot (1 - \exp(-b \cdot D))$$

where H is the observed H of the tree (in m), Hmax is a predicted maximum height (cm), b a constant (unitless) describing the sharpness of the curve and D the observed diameter at breast height.

This equation was fitted for each species in order to approximate the species specific Hmax. It should be noted that these are not site-specific estimates, as we assumed that the maximum height a species can achieve could be obtained at any given place. For some species the Hmax estimates were rather small just because of the trees that were found in our plots. For example an Hmax of 18.9 m for *F. sylvatica* is consider rather small with the literature reporting values up to 30m. We thus compared the Hmax estimates from the equation with a literature Hmax review, and in cases that were much smaller the mean values were used. These values were subsequently used in the traits table along with the rest of the characters used to define plant strategies.

Table 1: Summary of the H-D estimate of Hmax (fit), literature review of Hmax (lit) and value of Hmax used in the traits table (Hmax).

Species	Hmax_fit	b	N	Hmax_lit	Hmax
Abies borisii	20.99	0.05	242	40	30.49
Abies cephalonica	29.35	0.03	723	40	34.68
Acer spp	4.09	0.71	15	20	12.04
Carpinus orientalis	9.45	0.21	158	12.5	10.98
Castanea sativa	23.67	0.04	35	35	29.33
Certis siliquastrum	7.80	0.30	6	8	7.90
Cornus mas	8.42	0.27	28	10	9.21
Fagus sylvatica	18.91	0.08	694	40	29.45
Fraxinus ornus	9.89	0.19	8	25	17.44
Ilex aquifolium	3.04	0.64	30	15	9.02
Juniperus communis	4.91	0.27	21	7	5.95
Juniperus oxycedrus	3.50	0.57	357	7	5.25
Ostrya carpinifolia	13.84	0.07	6	24	18.92
Phillyrea latifolia	4.01	0.60	17	9	6.51
Pinus halepensis	6.96	0.09	9	25	15.98
Pinus nigra	26.49	0.04	936	40	33.24
Pistacia terebinthus	4.75	0.25	4	8	6.37
Pyrus spinosa	3.08	0.94	8	5	4.04
Quercus cerris	17.60	0.07	171	35	26.30
Quercus coccifera	8.86	0.14	133	15	11.93
Quercus frainetto	17.83	0.06	513	35	26.42
Quercus_ilex	8.79	0.23	9	25	16.90
Quercus pubescens	20.23	0.05	23	30	25.12

Seed Mass

Species specific seed mass data were extracted from various sources (Kew Botanical Garden (http://data.kew.org/sid/) and the BiolFlor (Kühn et al. 2004) databases). From the values extracted, we used the mean value per species as in some cases a relatively wide range between the reported values was observed. The following table (Table 2) summarises the values selected for the species of interest.

Table 2: Mean seed mass value for the species of interest

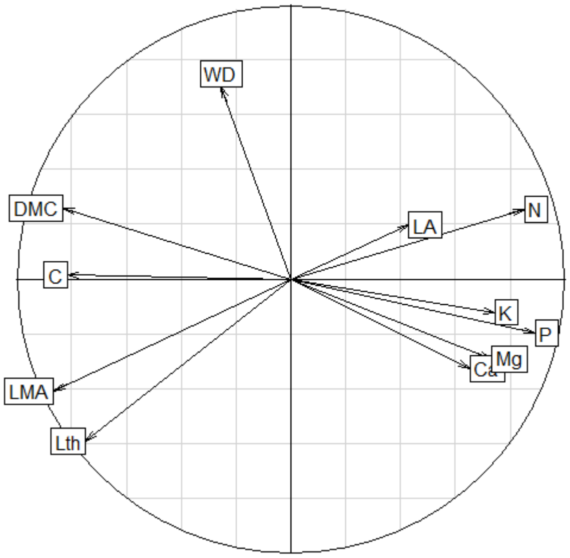
Genus	Species	Seed Mass (g)
Abies	*borisii-regis*	0.0560
Abies	*cephalonica*	0.0714
Acer	*campestre*	0.1123
Acer	*obtusatum*	0.0955
Acer	*platanoides*	0.1338
Arbutus	*andrachne*	0.1239
Arbutus	*unedo*	0.0046
Carpinus	*betulus*	0.0519
Carpinus	*orientalis*	0.0148
Castanea	*sativa*	7.6458
Cercis	*siliquastrum*	0.0277
Cornus	*mas*	0.3488
Cotinus	*coggygria*	0.0076
Cupressus	*sempervirens*	0.0072
Erica	*arborea*	0.0001
Fagus	*sylvatica*	0.2525
Fraxinus	*ornus*	0.0449
Ilex	*aquifolium*	0.0307
Juniperus	*communis*	0.0277
Juniperus	*oxycedrus*	0.2851
Ostrya	*carpinifolia*	0.0096
Phillyrea	*latifolia*	0.0332
Pinus	*halepensis*	0.0220
Pinus	*brutia*	0.0450
Pinus	*nigra*	0.0251
Pistacia	*lentiscus*	0.0265
Pistacia	*terebinthus*	0.0212
Platanus	*orientalis*	0.0044
Pyrus	*spinosa*	0.0320
Quercus	*cerris*	4.2149
Quercus	*coccifera*	3.6488
Quercus	*frainetto*	2.3093
Quercus	*ilex*	2.7254
Quercus	*pubescens*	0.6337

Numerical Techniques

The seed mass and Hmax dataset described above were integrated with the traits dataset measured during the MEDIT field campaigns and lab work. Thus a table fully describing 41 species in terms of leaf structure, chemistry seed mass and maximum height was available. However due to lack of fit of some light and CO_2 response curves this table was reduced to 30 species when biochemical leaf fluxes were considered. We applied a Principal Components Analysis on the full traits table, followed by a Ward Hierarchical Clustering on the species scores, to identify the optimum PFTs definition based on the traits that describe the species. This method was applied sequentially in order to validate the sensitivity of our technique to the addition of new traits. We thus started with leaf structural/chemical traits table, then enhanced the table with biochemical fluxes traits and finally included seed mass and maximum height.

The first PCA based on traits related to leaf structure and chemistry is shown in table 3. The first axis which explains 51.2% of the total variance is highly related to leaf thickness (L_{th}) leaf dry mass per area (LMA) and the concentrations of C, N, P, K and Mg. It thus reflects the classic leaf economic spectrum where plants with expensive leaves (high LMA) have lower nutrient concentrations and invest on longer term turnover of their investment. The second and third axes explain 12.6 and 11.7% of the total trait variance and are related to wood density (WD) and leaf area (L_A) and leaf dry matter content (DMC) respectively.

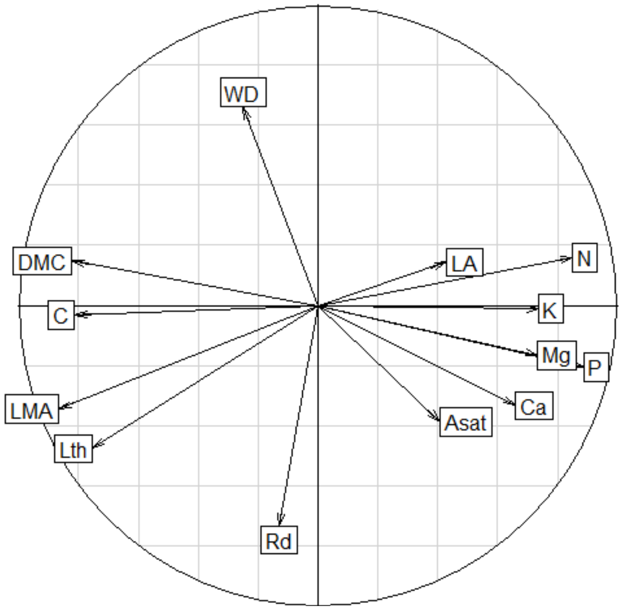
Table 3 and Figure 1: Summary of the PCA on leaf structural and chemical traits. Bold values represent traits that are highly correlated with the PCA axes.



Eigenvalue	5.631	1.385	1.286
Variance	0.512	0.126	0.117
L_A	0.494	-0.375	**0.657**
L_{th}	**-0.778**	-0.433	-0.349
DMC	-0.501	-0.214	**0.539**
LMA	**-0.865**	-0.301	-0.244
C	**-0.799**	-0.195	0.282
N	**0.871**	0.024	0.297
P	**0.886**	-0.245	-0.047
Ca	0.673	-0.212	-0.280
Mg	**0.730**	-0.275	-0.087
K	**0.736**	0.116	-0.319
WD	-0.267	**0.828**	0.154

In the second PCA, leaf light saturated photosynthesis (A_{sat}) and dark respiration (R_d) were included. The results of this analysis are summarised in the table 4 and figure 2. The first axis explaining 44.7% of the total variance reflect again the leaf economic spectrum. The second axis was related with WD and dark respiration. The third axis was associated with LA and DMC.

Table 4 and Figure 2: Summary of the PCA on leaf structural chemical and fluxes traits. Bold values represent traits that are highly correlated with the PCA axes.

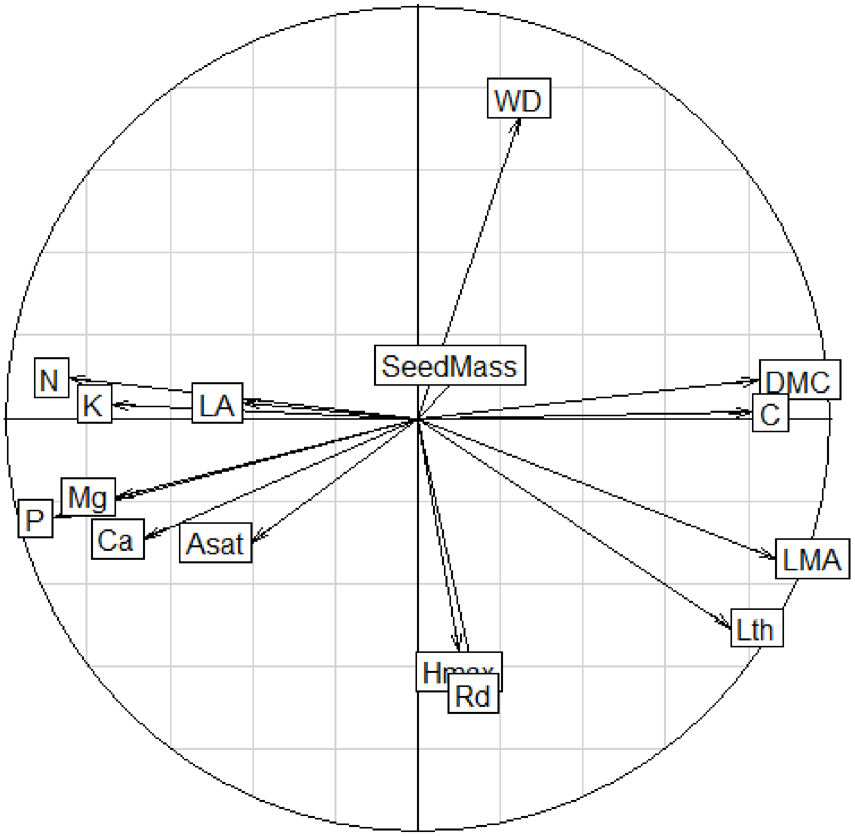


Eigenvalue	5.815	1.703	1.305
Variance	0.447	0.131	0.100
LA	0.494	0.035	**-0.752**
Lth	**-0.781**	0.416	0.154
DMC	-0.492	0.085	**-0.583**
LMA	**-0.862**	0.332	0.106
C	**-0.794**	0.104	-0.337
N	**0.869**	-0.090	-0.251
P	**0.882**	0.227	-0.037
Ca	0.682	0.319	0.180
Mg	**0.733**	0.192	-0.035
K	**0.729**	-0.054	0.339
WD	-0.263	**-0.677**	0.161
Asat	0.439	0.430	-0.024
Rd	-0.122	**0.745**	0.113

In the third and more representative PCA, where seed mass (S_M) and maximum height (H_{max}) where included the first three axes explained 65% of the total variance. Leaf economic relationships were captured on the first axis. The second axis was associated with H_{max}, S_M and DMC, suggesting that within our species pool taller trees do in general produce bigger seeds and have more conservative leaf strategies.). Thus they invest on a longer term payback of the resources they invest and the same slow return strategy is seen both at the leaf, the stem and seed plant component. Finally the third axis is associated with WD and S_M with denser wood species having bigger seeds.

The trade-offs identified along the three axes suggest that plant strategies can be allocated along a "fast-to-slow" economic spectrum (Reich 2014), reflected in our case at the leaf, the stem and size level. The three axes identified in this first PCA are by definition independent (orthogonal). We can thus suggest that both leaf structure, investment in regeneration and allometry can be used as basic dimension to describe a plant's strategy. Importantly these three dimension converge at the whole plant level to express the "fast-to-slow" economic spectrum.

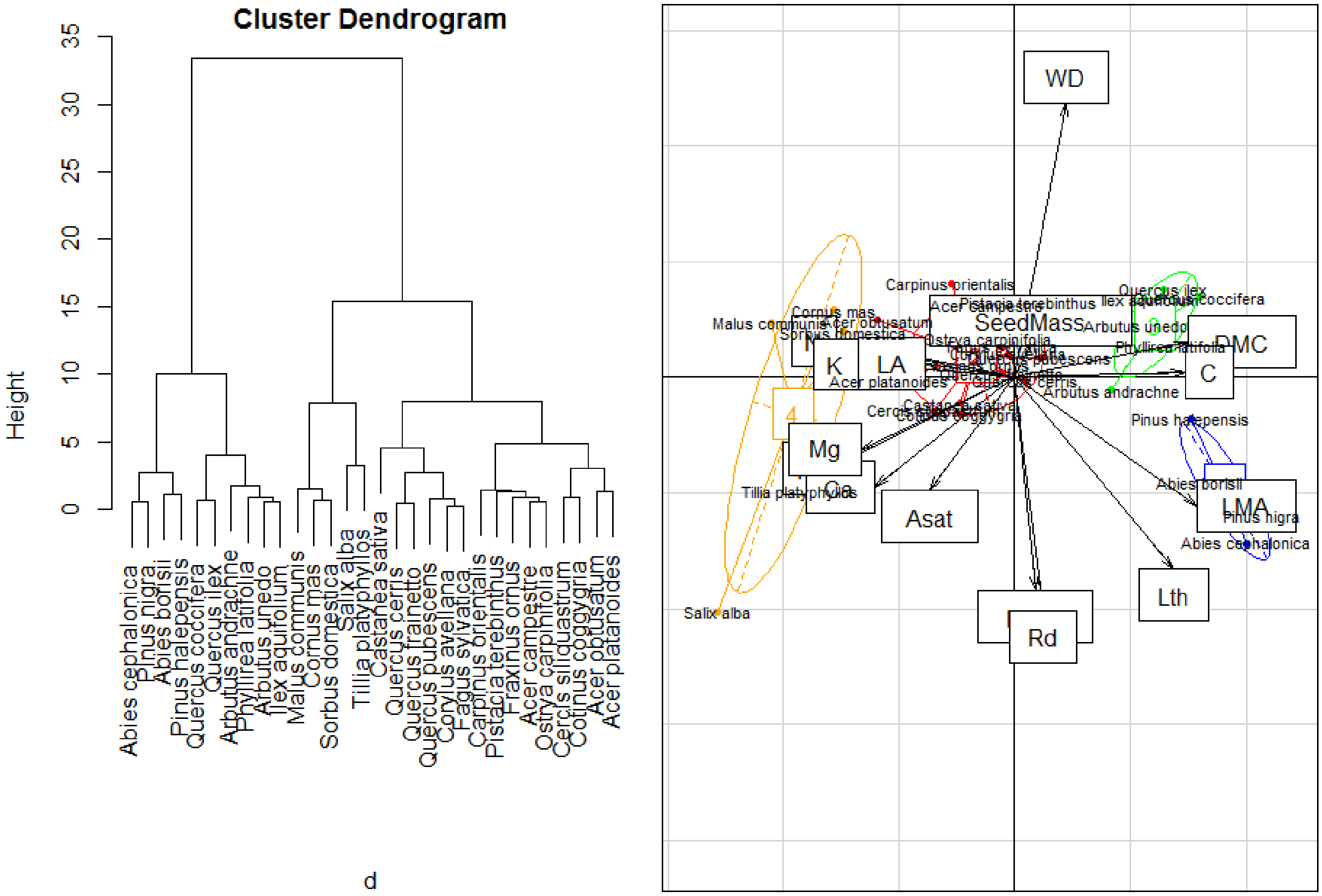
Table 5 and Figure 3: Summary of the PCA on all functional traits. Bold values represent traits that are highly correlated with the PCA axes.



Eigenvalue	5.83	2.21	1.72
Variance	0.39	0.15	0.11
Hmax	0.03	**-0.77**	-0.08
SeedMass	0.12	**-0.68**	**0.51**
LA	0.50	-0.37	0.32
Lth	**-0.78**	-0.25	-0.41
DMC	-0.48	**-0.60**	0.38
LMA	**-0.86**	-0.25	-0.27
C	**-0.79**	-0.17	0.10
N	**0.87**	-0.11	0.22
P	**0.89**	-0.23	-0.13
Ca	0.68	-0.04	-0.36
Mg	**0.74**	-0.28	-0.05
K	**0.72**	0.23	-0.14
WD	-0.26	0.39	**0.57**
Asat	0.44	-0.21	-0.26
Rd	-0.12	-0.32	-0.59

The species scores on the three axes of this PCA where then used as an input to a Hierarchical Clustering algorithm. The applied Wald algorithm uses the euclidean distance between species scores to group together species. The results of this analysis is provided in the following figure.

Figure 4: Cluster Dendrogram and PFTs based on species scores of the third PCA.

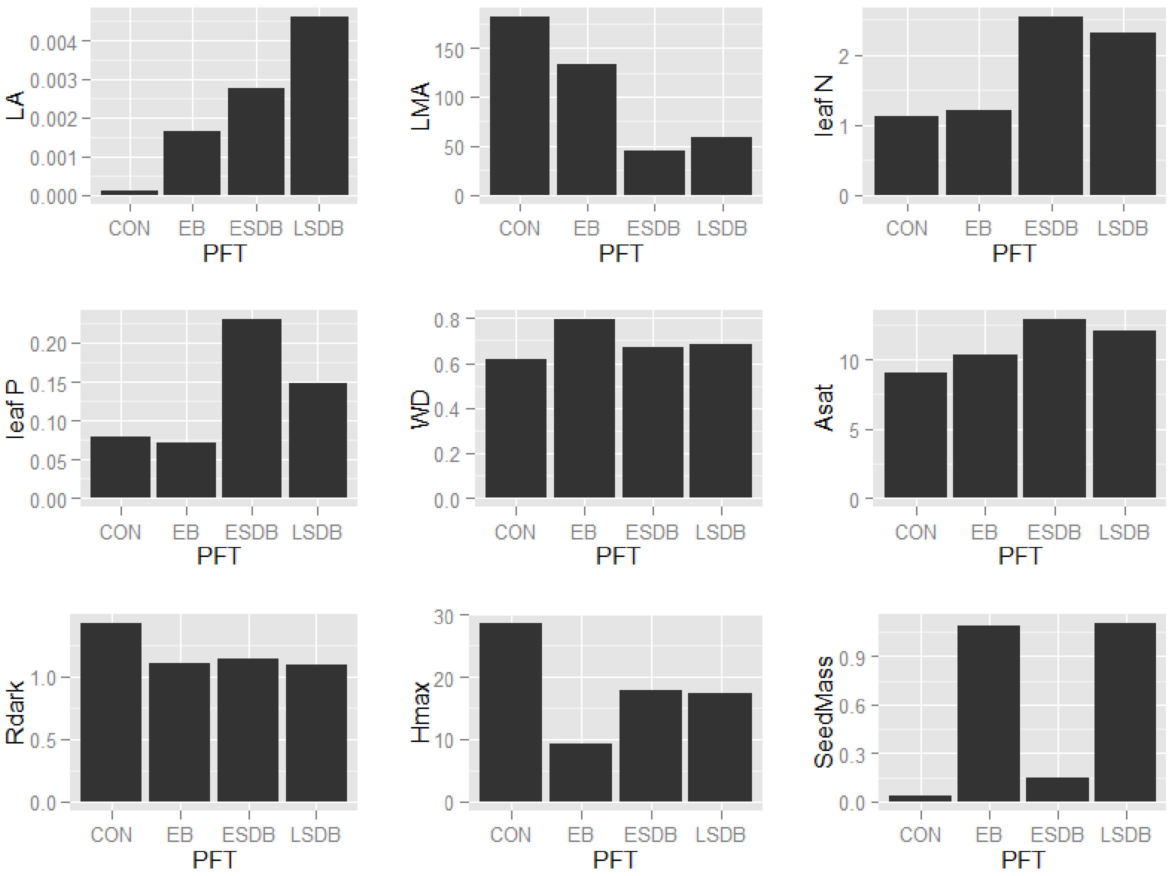


Four Plant Functional Types (PFTs) were identified based on their traits. The first PFT identified (blue) grouped together all conifer species (*P. halepensis, P. nigra, A. borisii-regis* and *A. cephalonica*). The second group (green) brings together all the evergreen sclerophyllous species (*A. unedo, A. andrachnae, Q. ilex, Q. coccifera, I. aquifollium* and *P. latifollia*). The first two groups are mainly separated based on the Hmax, Rd and WD, with the sclerophyllous group following a more conservative strategy (slower biochemical rates, higher WD). The third group (red) includes the majority of deciduous broadleaved species studied in MEDIT. These are separated from the fourth PFT (orange) based on their relatively smaller LMA and nutrient concentration.

Functional Description of the derived PFTs

We then used species classification to estimate the mean trait values for the newly derived PFTs. These are summarised in the following tables and figures and can be used to parameterise models of vegetation dynamics.

PFT	LA (m^2)	LMA ($g\ m^{-2}$)	DMC ($g\ g^{-1}$)	N (%)	P (%)	WD ($g\ cm^{-3}$)	Asat ($\mu mol\ m^{-2}\ s^{-1}$)	Rd ($\mu mol\ m^{-2}\ s^{-1}$)	gmax ($m\ s^{-1}$)
CON	0.00009	182.72	0.44	1.11	0.08	0.62	9.098	1.428	0.002
LSDB	0.00463	59.13	0.36	2.31	0.15	0.69	12.008	1.098	0.004
EB	0.00163	133.43	0.42	1.22	0.07	0.79	10.320	1.108	0.002
ESDB	0.00276	45.05	0.23	2.56	0.23	0.67	12.882	1.138	0.004



The derived PFTs present an elegant differentiation between life history strategies. The first group (CON) is grouping together all conifer species. These have the lowest LA but highest LMA and Hmax values and also illustrate the highest respiration rates suggesting that they follow a conservative strategy in terms of resource acquisition and use. The second group represent the evergreen sclerophyllous (EB) species which mainly differentiates from the CON group from the LA, LMA, WD and Seed Mass characters. The higher LA and lower LMA enables this group to achieve a relative higher photosynthetic rate. However their high WD values is associated with an increase ability to withstand disturbances. The high seed mass values reflects a conservative recruitment strategy. Our numerical method nicely revealed two discrete life history strategies for deciduous broadleaved species. The first of those groups is the early succesional (ESDB) type which illustrates a potential higher growth rate (N, P, Asat). This pioneer strategy is also reflected in low seed mass which is considered to be associated with higher fecundity. On the other hand the second deciduous broadleaved group (LSDB) is found on the other end of the plant economic spectrum, grouping together species with relatively higher (LMA) and lower N and P leaf concentrations to its deciduous counterpart. This conservative strategy is also seen in seed mass, where species are investing in safer and bigger seeds.

Discussion - Conclusions

In this report we presented a set of numerical methods applied to optimally identify PFTs for Mediterranean forests. The approach applied was based on a "first principles" rationale, i.e. we used a range of functional characters that are linked to fundamental plant properties/processes such as leaf resource allocation, photosynthesis/respiration and whole plant architecture, and explored to what extent these traits can be used to define PFTs.

Our results suggest that in general life form and taxonomy are sufficient to classify Mediterranean forest species found in Greece. By applying sequentially our numerical technique we show that the life form classification is maintained when new traits are included. This is in agreement with results from MEDIT Deliverable 7 (D5.1) where the greater variation in most of the functional traits under consideration was identified at the species level, i.e. the phenotypic variability. We can thus conclude that four PFTs can be used to group the species studied during the MEDIT field campaigns. These are:

- The conifer PFT, including large tree species with high fecundity and a relatively conservative leaf structure. These are more competitive compared with the evergreen PFT.
- The evergreen sclerophyllous PFT, including smaller species that invest in resource management that enables them to withstand resource scarcity and disturbances.
- The early successional deciduous broadleaved PFT, with higher growth rates and increased fecundity.
- The late successional deciduous broadleaved PFT, with slower growth rates and higher investment in seed size.

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