Climate, and not fire, drives the phylogenetic clustering of species with hard-coated seeds in Mediterranean Basin communities

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Abstract

Hardseededness is a common trait in Mediterranean plant communities, although the origin of its selection is controversial. It may be a mechanism of persistence to fire temperatures, but could also form part of a gap-detecting mechanism to provide germination cues under arid conditions. To disentangle this, we studied the phylogenetic structure of plant communities against fire frequency and aridity gradients. The phylogenetic structure in Mediterranean Basin ecosystems was analysed for the hardseededness trait as a whole and was separated by the families composing this trait (Fabaceae and Cistaceae). This study focused on woody perennial species. The phylogenetic structure was also contrasted against soil classes. Hardseededness on the whole, and for the Fabaceae family alone, showed phylogenetic clustering as aridity increased. Cistaceae displayed the opposite pattern with phylogenetic clustering in most humid areas, together with a significant soil effect. Surprisingly, fire frequency had no influence in any case. This climate-driven phylogenetic clustering indicates that the hardseededness trait could confer some fitness advantage under dry conditions. For this reason, coexisting species were more closely related in the community with increasing aridity. This effect was especially evident for the Fabaceae family. These results shed some light on the evolutionary selection of this adaptive trait under Mediterranean conditions. Our results question the role of fire in the selection of the hardseededness trait in Mediterranean Basin ecosystems and indicates that climate is the most important factor. Therefore, we should be cautious in assigning to fire a preponderant role in the selection of some plant traits.

Key words: Adaptive trait; Community assembly; Habitat filtering; Hard coat; Seeder; Soils.

1. Introduction

Habitat filtering is one of the most important processes that drives community assembly (Webb et al., 2002; Kraft et al., 2014). Under a set of environmental conditions, specific traits can confer advantages to some species *versus* others by allowing them to occupy a particular habitat. For example, in Mediterranean ecosystems, climate and geology (soils) have been traditionally considered the most fundamental forces of community assembly (Raven and Axelrod, 1978; Thompson, 2005; Ackerly, 2009). However, it has been suggested in recent years that fire can also be a factor of equal or greater importance in some cases (Verdú and Pausas, 2007; Keeley et al., 2012). In this ecosystem type, fire is a recurrent disturbance caused by hot dry summers that makes vegetation highly flammable (Keeley et al. 2012). Thus community composition can be formed mainly by these three factors interacting with the pool of species traits (Verdú and Pausas 2007, Ojeda et al. 2010).

Hardseededness (HS) is a frequent trait under Mediterranean conditions, but one that is also present in many species and ecosystems worldwide (Parker and Kelly, 1989; Baskin et al., 2000; Ooi et al., 2014; Willis et al., 2014; Rubio de Casas et al., 2017). In fire ecology studies, HS is associated (or considered synonymous) with the physical dormancy conferred by a hard-impermeable coat of palisade cells. This hard coat allows the formation of a persistent soil seed bank that can last for decades (Parker and Kelly, 1989; Baskin et al., 2000). The species with this trait are usually included in the so-called functional group of “seeders”, characterised by a pulse of germination and establishment after disturbances (Paula and Pausas, 2008). However, the origin of the selection of this adaptive trait is still controversial in Mediterranean ecosystems (Bradshaw et al., 2011; Keeley et al., 2011; Santana et al., 2013a). The selection of this trait has been long-since related to fire (Keeley, 1991; Moreira and Pausas, 2012). Indeed the HS trait allows seeds to withstand high temperatures, while these high temperatures break their impermeable coat and unleash a flush of germination at the same time (Paula and Pausas, 2008). This flush occurs when resources availability is high by the deletion of competing vegetation and the presence of a soil rich in nutrients through ash deposition (Keeley, 1991). However, it has been suggested that HS trait selection could be related to dry conditions, which are also typical of the Mediterranean climate (Baeza and Roy, 2008; Santana et al., 2013a). In the bare soil gaps created by disturbances, daily soil temperature fluctuations in summer can break the physical dormancy of soil-stored seeds (Baeza and Roy, 2008; Santana et al., 2013a; Ooi et al., 2014). This gap-detecting mechanism may be an adaptive advantage because it coordinates germination after summer, during the next wet autumn season, with enough time for seedlings to grow and establish before the next dry summer season (Santana et al., 2013a; Jaganathan, 2015). One key attribute suggested to distinguish between fire-adapted from gap-detecting species is the temperature threshold required to break seed dormancy (Moreira and Pausas, 2012; Santana et al., 2013a; Ooi et al., 2014). In species with obligate fire dormancy release, this threshold is closely related to temperatures that occur only during fires (80-100ºC), while in species with gap dormancy release would be related to temperatures typical from summer soil temperatures (40-70ºC) (Ooi et al., 2014). However, very little information is available about this temperature threshold, and further approaches are needed to clarify the role of different environmental factors in HS trait selection.

In the Mediterranean Basin (MB), the HS trait is a phylogenetic conserved trait that is present mainly in species from the Fabaceae and Cistaceae families (Verdú and Pausas, 2007). In this region, these families have been detected to date back to the Neogene period, but their presence intensified in the Quaternary, concomitantly with the definitive onset of a dry seasonal climate (Mediterranean climate) and frequent fires (Thompson, 2005; Rundel et al., 2016). The synchronised emergence of such factors does not clarify which of them was the most determinant driver of community assembly processes, and whether HS selection actually favoured the species with this trait. If environmental filtering was a dominant community assembly process, then the HS trait would be expected to be clustered (Webb et al., 2002);

that is, coexisting species would share a niche trait that confer them some advantage. In contrast, when environmental filters are absent, the community is shaped by competitive interactions and is characterised by phylogenetic overdispersion (Webb et al., 2002; Cavender-Bares et al., 2004). In the latter case, coexisting species are not closely related because they tend to avoid niche overlapping. According to these premises, the assessment of which environmental filter is the most determinant in clustering the HS trait, whether it is fire or climate, may shed some light on its adaptive selection. In other words, if HS is an important trait to be able to persist high fire activities or dry conditions, phylogenetic clustering would be expected to increase in gradients of these factors. Some weaknesses have been pointed out in using community phylogenetics to describe community assembly processes (Kraft et al., 2014; Gerhold et al., 2015), but these methods are still very valuable for addressing eco-evolutionary questions (Gerhold et al., 2015). In any case, this approach is not so simplistic and the major drawback for determining which factor (fire or climate) is the most determinant is that they are often conflated. On local and regional scales, both gradients often follow the same pattern with higher fire frequencies at dry and hot sites. For example, phenotypic and phylogenetic clustering of seeder species has been observed in the MB when comparing wet areas with low fire frequency to drier areas with higher fire frequency (Lloret et al., 2005; Verdú and Pausas, 2007). Nevertheless, if we are to know the relative importance of fire or climate on HS trait selection, it is essential that we distinguish between these two environmental gradients.

One plausible alternative to discern between fire activity and climatic gradients is the intermediate fire-productivity hypothesis (Van der Werf et al., 2008; Krawchuk and Moritz, 2011). This hypothesis suggests that, with an increasing gradient of aridity/productivity, fire activity peaks at intermediate levels by following a humped or unimodal relation. Here fuel and drought act as fire drivers along the aridity/productivity gradient; i.e., in moist-productive regions, fire activity is driven by frequency of droughts because fuel is readily available, while fire regimes are fuel-limited in unproductive-arid systems. This hypothesis has been tested and corroborated on different scales, ranging from regional (Pausas and Bradstock, 2007) to worldwide gradients (Van der Werf et al., 2008; Krawchuk and Moritz, 2011; Murphy et al., 2011), and also in MB ecosystems (Pausas and Paula, 2012). This hypothesis, therefore, presents an ideal framework to analyse the community assembly processes that derive from the environmental filtering of the HS trait by fire or climate.

It is noteworthy that fire and climate are not the only environmental factors to influence the phylogenetic structure of plant communities in Mediterranean ecosystems. Soils can also play an important role in these processes because they influence resource availability (Dantas et al., 2015). In soils that are infertile or possess a low water retention capacity, the traits that enhance seedling survival may also be fundamentally valuable. Indeed the HS trait can imply an advantage through the conferred bet-hedging strategy (Venable, 2007). Persistent soil seed banks, which annually release a small proportion of seeds to germinate, spread the risk of seedling establishment failure over time (Fenner and Thompson, 2005). Indeed it has already been observed that infertile soils can locally promote the phylogenetic clustering of the “seeder” trait in MB ecosystems either by themselves or via an interaction with fire (Ojeda et al. 2010). Therefore, studies that determine the phylogenetic structure of plant communities should not neglect the influence of soil on community assembly processes.

The aim of this paper is to assess the role of fire, climate and soils on filtering the presence of the HS trait in MB ecosystems. Our experimental design allowed us to define two different and contrasting gradients of aridity and fire in the SE Iberian Peninsula: (i) a climatic gradient of increasing temperatures and decreasing precipitation; (ii) a unimodal fire activity gradient where higher frequencies occur at intermediate climatic gradient values (following the fire-productivity hypothesis). We hypothesised that if fire predominated as the filtering force, the phylogenetic clustering of the HS trait would follow a unimodal pattern on the aridity gradient. In contrast, if climate was the most determinant force, phylogenetic clustering would increase with aridity. We also included the relation between the phylogenetic structure of communities and soil properties in this analysis. If it was a determinant, phylogenetic clustering would increase with both soil infertility and lower water retention capacity. Disentangling which factor plays a more determinant role in the phylogenetic clustering of the HS trait could shed some light on the evolutionary selection of this trait. The hypotheses herein proposed were tested for the HS trait on the whole, and were separated by the families composing this trait (Fabaceae and Cistaceae). We intended to see if a differential response corresponded to the intrinsic characteristics of the studied families.

2. Material and Methods

2.1. Study area and vegetation data

This work centred on the Valencia Region (Eastern Iberian Peninsula; 22885 km^2; Figure 1), which has a typical Mediterranean climate where forest fires are recurrent episodes. To study the phylogenetic structure of the HS trait at the community level, we obtained the data collected by the "Banc de dades de la Biodiversitat de la Comunitat Valenciana" (http://bdb.cma.gva.es, last accessed in March 2014). This is a biodiversity bank data managed by the Regional Valencian Government which, for each 1×1 UTM coordinate, collects all the plant and animal species historically cited for this point. This bank has more than 19,000 species and 1,750,000 species detections throughout the region. This makes it an excellent tool to assess the presence of species at the spatial level and for macro-ecological studies. For this study, all the plant species present in the bank data were named and classified as life forms (following Raunkiaer, 1934) according to the flora described for the whole Valencia Region by Mateo and Crespo (2001). Only woody perennial biological types (i.e., chamaephytes and phanerophytes) were used. Species from coastal ecosystems or those typical of specific ecosystems, such as riverlands and salt marshes, were removed, along with cultivated, naturalised and exotic species. As the dataset is composed of individual observations of species for each 1×1 UTM coordinate, thus they do not have equal sampling efforts, we used the species presence-absence data matrix for 10×10 UTM. This smaller work scale resulted in a reduction in the species-absence bias and ensured a representative dataset of species presence. We took the sum of all the species present in this coordinate as the corresponding community for each 10×10 UTM. Then we confirmed that each coordinate had representative descriptions of the community composition by calculating the species accumulation curve. We assumed that all the coordinates contained a representative community composition as they achieved an equilibrium with an asymptote. The UTM coordinates that did not meet these assumptions were removed from the analysis. These coordinates were mainly those on the border limits of the region or in coastal areas with small areas to be sampled, as well as the coordinates for which most of their area had been urbanised (i.e., city of Valencia and conurbations). Finally, we used 202 UTM coordinates for our study.

2.2. Climatic gradient

The climatic conditions for each 10×10 UTM coordinate were defined by including the values of the mean annual precipitation (PP) and the mean annual temperature (T) in the database (Pérez-Cueva, 1994). The whole of the Valencia Region is characterised by having a wide range of aridity conditions. For example, the mean annual precipitation ranges from 817 mm to 217 mm, and comprises semiarid, dry subhumid and humid Mediterranean climates (Trabucco and Zomer, 2009). The mean annual temperature also considerably varies from 10ºC to 19ºC. As a climatic proxy of the aridity conditions, we used the Rainfall Index of Lang (1915) as the quotient PP/T, which is considered one of the simplest and most direct ways of describing this variable. The climatic gradient defined for the Valencia Region roughly follows a North to South pattern, with some variability as a result of mountain ranges and its proximity to the sea (Figure 1). Altitude ranges from 1,813 m to sea level.

2.3. Fire gradient

The fire activity in the Valencia Region follows a humped pattern along the defined aridity gradient (Figure 2). The fire gradient follows the intermediate fire-productivity hypothesis, with low fire activity in semiarid areas and humid areas as a result of biomass limitation and the low frequency of fire-prone dry conditions, respectively (Pausas and Paula, 2012). Fire activity concentrates mainly in intermediate areas, where a dry subhumid climate dominates. We defined this humped pattern by two different proxies: number of fires (Nfires) and total area burned (Burnt_area) since 1993. These data were provided by the regional environmental services for each 10×10 UTM coordinate, and the two proxies were compared to the above-described PP/T climatic index (Figure 2). Data included both natural and man-caused fires.

2.4. Soil properties

For each 10×10 UTM, a percentage of the area was occupied by different lithology classes (COPUT, 1998). Therefore as a determinant of soil properties, we used these lithology classes categorised into 11 different types: Limestones (36% of total area), Gravels (21%), Dolomites (11%), Limes (8%), Marls (8%), Clays (5%), Conglomerates (5%), Sands (4%), Sandstones (3%), Metamorphic (0.3%), Volcanic (0.01%). In order to include the soil differences in each 10×10 UTM, we performed a principal components analysis (PCA) with standardised data values. The site scores of the first and second PCA axes were used as proxies of soil variability. The first axis explained 15% of soil variability, while the second axis explained 13% (Figure S1 in the Supplementary Material). PCA 1 showed a gradient of soils dominated by limes towards the soils dominated by clays (left to right), with intermediate values dominated by Sands, Gravels, Marls and Limestones (Soil_PCA1 hereafter). The PCA 2 axis showed a pattern that went from positive values dominated by Limestones, Marls and Conglomerates to negative values dominated by Sandstones, Sands and Gravels (Soil_PCA2 hereafter).

2.5. Data analysis

All the statistical analyses were performed in the R statistical environment (version 3.3.2 R Core Team, 2016). Phylogenetic analyses were done using the packages *brranching* (Chamberlain, 2016), *ape* (Paradis et al., 2004), *phytools* (Revell, 2012) and *picante* (Kembel et al., 2010). The tree was visualised using *ggtree* (Yu et al., 2017). The phylogenetic analyses of the DNA data were conducted on the CIPRES Science Gateway (Miller et al., 2010) and processed with R packages. The multivariate analysis was performed with the *vegan* package (Oksanen et al., 2017), while the generalised additive models were fitted using the *mgcv* package (GAM; Wood, 2011).

2.6. Phylogenetic analysis

For the whole presence-absence data matrix (432 species), we assigned a qualitative state of the HS trait (yes/no) to each species. In the MB, this trait is restricted to species from the Cistaceae and Fabaceae families in woody perennial species (Baskin and Baskin, 2014). As we were unable to ensure the proper assignment of the HS trait to herbaceous species, we focused our study on woody perennial species. Not in vain, woody perennial species are the main component of the composition and structure of the studied Mediterranean vegetation. We had 90 species with the HS trait, 35 from Cistaceae and 55 from Fabaceae.

Afterwards, a phylogenetic tree was assembled for the 432 species included in the dataset (Figure S2). For this purpose, we used the *phylomatic* function from the *brranching* package. We constructed a tree by grafting families, genera and species onto the angiosperm tree R20120829 for plants (Chamberlain, 2016). Once the tree was assembled, it was checked for polytomies and resolved whenever possible. Branch lengths were adjusted by Grafen's method (Malhado et al., 2015), and then it was forced to be ultrametric (function *force.ultrametric* from the *phytools* package).

Secondly, we used DNA sequences to create a more resolved tree to reduce some of the unresolved polytomies of the previous tree. Here data mining was done in the public database GenBank to search for relevant sequences. Only one sequence per species was downstreamed, and we were able to collect 245 sequences containing the 18S, 5.8S genes, the complete ITS marker and of similar length. The multiple sequence alignment algorithm MAFFT (Katoh et al., 2005), available on the EMBL-EBI portal (http://www.ebi.ac.uk/Tools/msa/mafft/, last accessed December 2019), was used to align the 245 sequences. The Maximum Likelihood analyses were conducted using the RAxML HPC2 (Stamatakis 2006) in the XSEDE tool (Phylogenetic tree inference using maximum likelihood/rapid bootstrapping run on XSEDE) employing a GTR + G+ I substitution model. To assess the statistical support of clades, 1,000 fast-bootstrap (BS) replications were run according to the GTR-CAT approximation. However, we were unable to retrieve the sequences for all the species (i.e., 247 species of 432; 57% of all species). Here 110 species were added to their genus over this tree using the species genus by defining a function based on the *add.species.to.genus* function of the phytools package (Figure S3). Finally, we decided to utilise this phylogenetic tree based on DNA to resolve the polytomies of some species from a previously built complete phylogenetic tree, and use it as the working tree (Figure S2).

Initially, the phylogenetic structure of communities was assessed by calculating the mean pairwise distance (MPD) of species with the HS trait included in each 10×10 UTM against the MPD values obtained with a null model. Here the *ses.mpd* function (*picante* package) for the richness data with a null-model of *taxa.labels* was used. This method reshuffles the species labels across the above-assembled phylogenetic tree. Finally, in order to account for the possible effect of different sampling efforts on species richness among sites, we derived the net relatedness index (NRI) for the species with the HS trait, which is the standardised effect size of MPD *vs.* null MPD (Webb et al., 2005). The NRI standardises the differences between the average phylogenetic distances in the observed and null communities by the standard deviation of the phylogenetic distances in null communities (Webb et al., 2005). The NRI rises with increasing clustering and becomes negative with overdispersion (Webb et al., 2005). The

NRI evaluation of the Cistaceae and Fabaceae families was made by repeating the analysis, but by considering only the species of each family.

2.7. Phylogenetic structure against the climate, fire and soil gradients.

To test our hypothesis about the main drivers of phylogenetic clustering of the HS trait, we used GAM models. We examined how the HS trait, and the Cistaceae and Fabaceae NRI, are related to the climate (PP/T index), soil (Soil_PCA1, Soil_PCA2) and fire variables (Nfires and Burnt_area). This approach was chosen because it makes no *a priori* assumption about the functional relation between variables (Wood, 2011), and depicts the real trend with no restrictions. We considered that the phylogenetic structure was climate-driven if HS clustering increased linearly with the climatic gradient. However, if it was driven by fire, phylogenetic clustering would follow a hump-shaped pattern. Similarly, if soil was a determinant factor, the phylogenetic structure would vary along the PCA soil gradients.

For each NRI (HS trait, Cistaceae and Fabaceae), we started fitting the null GAM model, and then all the explanatory variables were added sequentially until the fully parameterised model was fitted. Thin plate regression splines with shrinkage terms were used as the basis for smooth climate, fire and soil explanatory variables. We simultaneously accounted for spatial autocorrelation by including the coordinates of points (i.e., Latitude and Longitude) as smooth interaction terms (Wood, 2011). Prior to GAM modelling, we eliminated the outliers and extreme observations to reduce leverage using Cook's distance (Alimadad et al., 2011). We then ranked models according to their Akaike's information criterion (AIC) and Bayesian information criterion (BIC). The models with lower AIC and BIC values and the fewest estimable parameters were considered the “best models”. Here complex models were considered a candidate model only if they had two AIC units less than the AIC of all their simpler nested models (Burnham and Anderson, 2002). We simultaneously tested that the variance inflation factor of the selected models was below 3, which indicates lack of collinearity issues (Dormann et al., 2013). We used likelihood ratio R^2 and deviance proportion as measures of the variance that the model explained.

Finally, in order to know the weight of the explanatory variables in determining the NRIs (HS trait, Cistaceae and Fabaceae), all the variables were classified into four general components of influence: climate variables (PP/T), soil variables (Soil_PCA1, Soil_PCA2), fire variables (Nfires and Burnt_area) and spatial variables (Latitude, Longitude). Then two full models of three components were defined: a first one with the climate and fire variables as the main drivers, and a second model with climate and soil:

1) yi= a + s1(Latitude, Longitude) + s2(PP/T)+ s3(Burned_area)+ s4(Nfires)

2) yi= a + s1(Latitude, Longitude) + s2(PP/T)+ s3(Soil_PCA1)+ s4(Soil_PCA2)

Thus partial deviances were calculated sequentially by removing the predictors corresponding to space, fire, climate and soil from these models. These partial deviances were a proportion of the total model deviance explained by each component (Wood, 2011). Models were refitted after the sequential elimination of components, in which two full models of three components each were evaluated instead of a full model with the four components to reduce the number of sequential possibilities.

3. Results

3.1. HS trait

Using generalised additive models, we were able to select the best NRI model for the HS trait based on AIC, BIC and the fewest number of estimable parameters (df). This model included the space (Latitude, Longitude) and climate (PP/T), but not the fire or soil variables (Table S1a). The selected model explained a large proportion of deviance (40%; R^2= 0.35), and the PP/T predictor was significant (edf=5.39, F=6.50, $p<0.001$). The NRI showed a linear decrease from the positive clustered sites at lower PP/T values to the negative overdispersed sites, which were stable around -0.5 with medium and high PP/T values (Figure 3). This meant that HS clustering increased as aridity rose. Surprisingly, the fire variables were poorly related to the NRI, did not appear in the best models and showed no humped pattern as predicted.

We divided predictors into groups of variables to represent space (Latitude, Longitude), climate (PP/T), soil (Soil_PCA1 and Soil_PCA2), and fire (Nfires and Burnt_area). We followed a deviance partitioning approach to identify the unique contributions of each general component to the HS trait NRI. The results showed that space explained 27-28% of the total explained deviance, and climate, soil and fire explained approximately 15-16%, about 4%, and only 3%, respectively (Table 1a). These values indicated that the climatic gradient was the main environmental variable that explained HS trait phylogenetic clustering variability despite the strong influence of the spatial gradient.

3.2. Fabaceae and Cistaceae responses

The best NRI model for Fabaceae also included the space (Latitude, Longitude) and climate (PP/T), but not the soil or fire variables (Table S1b). This model explained a large proportion of deviance (49%; R^2= 0.45), and all the included predictors were significant: space (edf=7.94, F=2.13, p=0.019) and climate (edf=6.88, F=7.55, p<0.001). The NRI showed a similar response to the HS trait, with a linear decrease from the positive clustered sites at lower PP/T values to the negative overdispersed sites at higher PP/T values (Figure 3). For Fabaceae, when the predictors were divided into groups of the variables representing space (Latitude, Longitude), climate (PP/T index), soil (Soil_PCA1 and Soil_PCA2) and fire (Nfires and burnt_area), the results once again showed that the spatial (24-26%) and climate (20-23%) patterns mainly explained phylogenetic clustering, followed at some distance by the soil (6%) and fire (3%) variables (Table 1b).

The Cistaceae NRI best model based on AIC, BIC and the fewest estimable parameters (edf) included space (Latitude, Longitude), climate (PP/T) and soil (Soil_PCA1) (Table S1c). The model explained a large proportion of deviance (69%, R^2= 0.64), and all the included predictors were significant: space (edf=19.90, F=4.95, p<0.001), climate (edf=4.40, F=2.60, p<0.022) and soil (edf=1, F=11.06, p=0.001). Here the inclusion of fire did not considerably improve either the AIC or BIC in the model (Table S1c). The NRI was clustered at the sites with higher PP/T values, and lowered and remained overdispersed with values below 40 PP/T (Figure 3). Regarding soils, the NRI clustered in the more negative Soil_PCA1 values and moved linearly to overdispersion towards the positive values (Figure S4). It showed a spatial distribution for the clustered NRI values (>0) located in the northern part of the territory, and lowered towards the central and southern regions where the Cistaceae NRI was overdispersed (<0) (Figure 4). For Cistaceae, when predictors were divided into groups of variables representing space (Latitude, Longitude), climate (PP/T), soil (soil_PCA1 and soil_PCA2) and fire (Nfires and Burnt_area), the results revealed that the spatial (32-39%) and climate (20-27%) patterns chiefly explained Cistaceae clustering, followed by the soil variables at some distance (17%) and then by the fire variables (2%) (Table 1c).

4. Discussion

Phylogenetic clustering did not follow the unimodal gradient followed by fire in our study area in any case, which questions its role in HS trait selection in MB ecosystems (Verdú and Pausas, 2007; Moreira and Pausas, 2012). Our results better agree with the classic point of view that climate and soils are the main drivers of community assembly processes in Mediterranean ecosystems (Raven and Axelrod, 1978; Thompson, 2005; Ackerly, 2009; Keeley et al., 2012). These results support the view that we should be cautious to assign a preponderant role to fire in the selection of plant traits in some cases (Bradshaw et al., 2011). Of all the study variables, climate was the main driver of the phylogenetic structure for the HS trait in MB communities. Phylogenetic clustering for the whole HS trait followed an increasing pattern as aridity rose, which was especially evident for the Fabaceae family. Conversely, the Cistaceae family followed a different pattern by showing phylogenetic clustering in the most humid areas, as well as a significant soil type effect. The spatial component also explained a large proportion of HS trait variability as a result of the similarity expected between neighbouring communities (spatial autocorrelation) and other factors not herein considered, such as dispersal ability, species extinction or historic land use.

HS is inherent for species from the Fabaceae and Cistaceae families in the MB. The presence of these families in this area was first observed during the Neogene (Thompson, 2005). The *Genista* and *Astragalus* genera (Fabaceae) appear in Pliocene records (Pignatti, 1978; Thompson, 2005) when the climate seasonality onset of the Mediterranean climate intensified (Suc, 1984). Similarly, the molecular clock places the origin of the *Fumana* and *Helianthemum* genera (Cistaceae) during the Miocene (Guzmán and Vargas, 2009). Palynological records of Cistaceae species have been dated for the Miocene, and were probably hosted in semiarid open vegetation spots when the tropical climate began to undergo seasonal variation (Thompson, 2005; Jiménez-Moreno, et al. 2010). It was during this transition between the Neogene (Pliocene) and the Quaternary (Pleistocene) when climate became drier, and many paleotropical and mesic temperate forest taxa disappeared to give way to a similar Mediterranean type vegetation to that which exists today (Rundel et al., 2016). This definitive onset of Mediterranean climate may have intensified habitat filtering and community assembly processes, and adaptive radiations of species from the Cistaceae and Fabaceae families may have occurred (Guzmán et al., 2009). In this case, the HS trait may have been an advantage under Mediterranean-dry conditions, which may be fundamental for determining the current phylogenetic structure of plant communities.

Our results support the hypothesis that climate is a determinant evolutionary force in the selection of HS in MB flora, or at least for the Fabaceae family species where the presented results are more evident. HS trait selection could have been the result of the adaptive advantage of being a gap-detecting mechanism that coordinates germination after summer.

Daily soil temperature fluctuations that rose in bare soils would break the physical dormancy of seeds to allow subsequent germination (Baeza and Roy, 2008; Santana et al., 2013a). The advantage here would be to predispose seeds to germinate during the wet autumn season, when shorter days and lower temperatures would help to keep soil moisture. It would be then when non-dormant seeds would be imbibed and germinate with enough time for them to establish and grow before the next limiting dry season (i.e., summer). HS also allows the formation of a persistent soil seed bank with numerous viable seeds that overcome plant life to ensure persistence in stressful environments (i.e., seasonal droughts in this case). Indeed this persistent seed bank enables a bet-hedging strategy to be incorporated; i.e., temperature fluctuations only break the dormancy of a proportion of the seed bank, so seeds do not germinate all at once (Venable, 2007). In this way, the risk of seedling establishment failure would spread over time and thus ensure further germinations in following years under more favourable conditions (Fenner and Thompson, 2005). In this sense, it would be interesting to ascertain which of these dormancy dimensions has been more important for HS selection: bet-hedging or synchronous germination. Bet-hedging would be related to high aridity conditions, and synchronous germination to high precipitation seasonality. Our results are restricted to woody perennial species which are expected to live more than 1 year and, thus, synchronous germination is key to overcome the limiting first summer. It is well-known that woody perennial species germinate mainly under long wet conditions, especially Autumn but, for example, germination is nil after summer storms (Santana et al., 2012). A different case would be herbaceous species, which are able to germinate and establish after sudden summer storms. Here the bet-hedging dimension, which avoids losing all seeds in a single unfavourable event, may gain relevance. For this reason, further studies are necessary to ascertain the phylogenetic community patterns of herbaceous species and to compare them with woody species. In temperate ecosystems, for some herbaceous species it has been observed that cold stratification produced by winter conditions is needed to break their physical dormancy, and not only high temperature fluctuations (Van Assche et al., 2002). In relation to herbaceous species, these points remain to be tested in MB ecosystems, but should be considered to interpret our results and future studies.

Lack of germination that is exclusively dependent on fire temperature (fire-dependent) in MB species may also support the climate hypothesis as a selective force of HS. For example, the seeds of *Ulex parviflorus* (Fabaceae) and *Cistus albidus* (Cistaceae) significantly germinate under summer conditions in open vegetation gaps (Santana et al., 2013a). The daily soil temperature fluctuations in these gaps in summer reach values of 65-68ºC, which suffice to enhance germination in this place and contrast with the temperatures that seeds found under vegetation (Santana et al., 2013a). It is also well-known that a germination flush in these families (Fabaceae and Cistaceae) occurs after disturbances other than fire; e.g., clearings and mechanical brushings (Paynter and Flanagan, 2004; Baeza and Roy, 2008; Santana et al., 2013a). These species are also involved in other different ecological processes from post-fire regeneration; e.g., they are considered good colonisers of open spaces and typically occur in early succession stages in abandoned fields (Tatoni et al., 1994; Gallego et al., 2004; Duguy and Vallejo, 2008). Laboratory studies indicate that simulation of soil temperature fluctuations is effective in breaking the physical dormancy of a significant proportion of dormant seeds from the Fabaceae and Cistaceae families (Baeza and Roy, 2008; Moreira and Pausas, 2012). However, very few works have investigated these thresholds for the wide range of species from these families in the MB.

Unlike the few works that have dealt with summer temperature fluctuations, there is a long-standing history of works that have studied germination response to simulated fire temperatures in the laboratory for MB species (See Paula and Pausas, 2008 and references therein). In short, it has been widely observed that maximum germination rates occur at fire temperatures (e.g., >80ºC). These observations have led to suggest that fire is a determinant factor in HS trait selection in MB species (Moreira and Pausas, 2012). However, this contrasts with the fact that no relation was herein found between fire activity and phylogenetic clustering on a regional scale. In fact the highest clustering appeared in the most arid areas, characterised by little fire activity and high temperatures. Some explanation of the minor role of fire, compared to climate, in affecting phylogenetic clustering can be found in: (i) dormancy temperature thresholds; (ii) the bet hedging capacity of species. Ooi et al. (2014) classified species with germination after summer temperatures into the functional group of "facultative pyrogenic dormancy release"; i.e., they are able to germinate under both conditions (fire and summer temperatures). These species commit a proportion of *ca.* 20% of seeds to germinate after summer temperature treatments and leave a large seed bank remaining. Conversely, fire-related temperatures (>80ºC) produce high germinations rates and a limited proportion of seeds remains dormant. This fact questions the advantage of high post-fire germination rates. Post-fire high seed bank depletion may jeopardise regeneration under extreme drought conditions by killing germinated seeds. If recurrent fires occur, the seed bank may also undergo significant depletions and species extinction. This suggestion falls in the line with the response to recurrent fires observed in MB ecosystems. For example, dense *Ulex parviflorus* gorse forms after a first fire in abandoned crop fields. However, recurrent fires (two and three fires in two decades) do not enhance the presence of this species, but lead to a drastic reduction (Santana et al., 2013b). A similar pattern has been found for *Cistus* species in NE Spain with increased abundance after one or two fires, but a drastic decline occurs after three, four and five recurrent fires in three decades (Vilà-Cabrera et al. 2008).

It is noteworthy that the phylogenetic structure of the Cistaceae family did not completely follow the expected pattern; i.e., it showed some phylogenetic clustering in northern humid areas. Investigating the phylogenetic structure using isolated traits, as in this study, may not always be an effective approach. Environmental effects on particular traits might not be independent of other traits due to evolutionary trade-offs (Herrera, 1992; Gerhold et al., 2015). This could be particularly relevant in the Cistaceae family, which gathers a significant number of structural traits to face water deficit; e.g., traits to improve water use efficiency and to uptake resources in leafs and roots (Paula and Pausas, 2006, 2011). Therefore, a multivariate approach to gain an in-depth understanding of the evolutionary trade-offs of Cistaceae could be interesting to disentangle this unexpected pattern, as well as the selection of the HS trait and other traits related to drought tolerance. At the same time, interactions with other environmental variables (e.g., soils) may also affect the phylogenetic structure. Further studies may be needed to assess if local endemisms, with specific traits that allow them to live under restricted soil conditions, may affect this pattern. For example, Cistaceae have a significant number of soil-driven vicariants (Mateo and Crespo, 2001), a point that could explain the selection of soil as an explanatory variable in our model, and the large proportion of the variance explained by this variable (17%) regarding the phylogenetic structure of communities.

These results for the MB contrast with other Mediterranean type ecosystems, where fire-dependent regeneration has been observed for different species with HS. In Californian chaparral, for example, species from the *Ceanothus* (Rhamnaceae) genus only germinate if seed banks face temperatures generated during fires (Keeley, 1991). In this case, HS has been considered to emerge much earlier as an adaptation to fire than to Mediterranean dry climate under the fiery conditions of the Neogene period (Pausas et al., 2006). Along the same line, the germination response of some species from the *Acacia* genus (Fabaceae) in Australian ecosystems are restricted to fire temperatures over 90ºC (Ooi et al., 2014; Cochrane, 2017). In these cases, adaptation to fire seems clearer as species undergo pyrogenic dormancy release, which only commits a proportion of their seed bank and permits bet-hedging mechanism efficiency to be preserved (Ooi et al., 2014). However, it is worth noting that species with fire-dependent regeneration are accompanied by many other species, which display facultative dormancy release and behave as opportunistic species by germinating and colonising open gaps when fire is absent (Keeley et al., 2006; Ooi et al., 2014). So it would be interesting to follow similar approaches to that herein presented in these Mediterranean type ecosystems as they could shed some light to clarify if the post-fire germination flush that occurs in gap-detecting species is an exaptation rather than an adaptation to fire, as suggested for MB ecosystems. This could also provide insight into the evolution of fire-dependent germination: whether it appeared in older lineages prior to the Mediterranean conditions under fiery conditions (as suggested for Chaparral species), or whether it was selected by starting from an adaptation to arid conditions that evolved towards a fire-adaptive trait, which may have also occurred for some Australian species of the *Acacia* genus.

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TABLES

Table 1. Deviance explained by the GAM models with the included environmental predictors. Model 1 includes fire as a predictor, while Model 2 includes soil as a predictor instead of fire.

	Model 1			Model 2		
	Predictor	Partial Deviance	SE	Predictor	Partial Deviance	SE
(a) HS Trait	All	0.47	-	All	0.46	-
	Space	0.28	0.07	Space	0.27	0.07
	Climate	0.16	0.07	Climate	0.15	0.01
	Fire	0.03	0.03	Soil	0.04	0.07
(b) Fabaceae	All	0.52	-	All	0.50	-
	Space	0.26	0.08	Space	0.24	0.07
	Climate	0.23	0.07	Climate	0.20	0.03
	Fire	0.03	0.003	Soil	0.06	0.07
(c) Cistaceae	All	0.68	-	All	0.69	-
	Space	0.39	0.12	Space	0.32	0.11
	Climate	0.27	0.11	Climate	0.20	0.10
	Fire	0.02	0.012	Soil	0.17	0.08

FIGURES

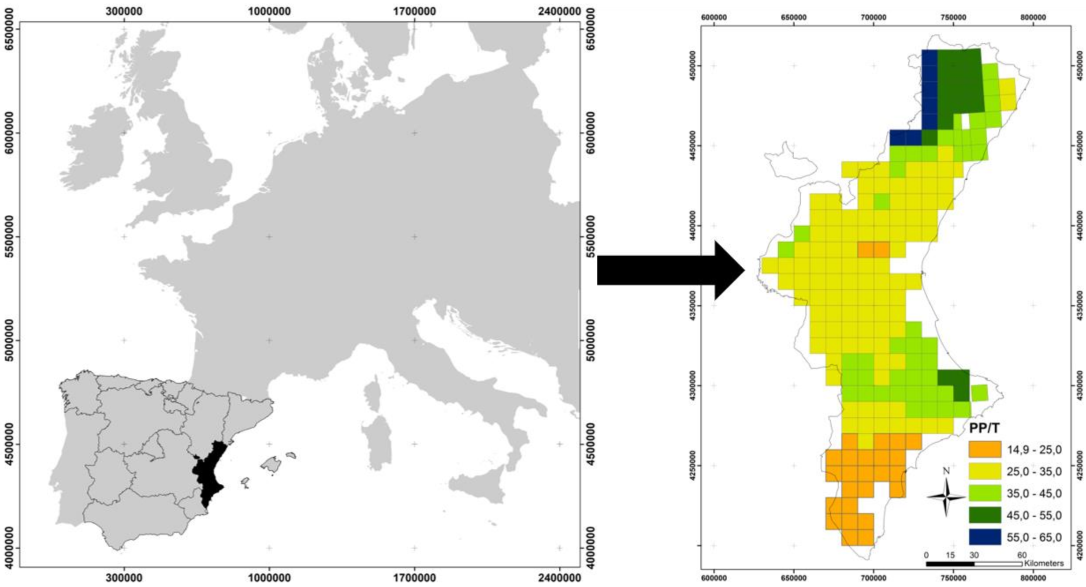

Figure 1. Location of the study area (left). The climatic gradient is depicted by the 10×10 UTM coordinates used in the study (right). The climatic gradient is described by the Rainfall index of Lang (1915) as quotient PP/T (PP = mean annual precipitation; T = mean annual temperature). The numbers on the edge of figures indicate UTM coordinates.

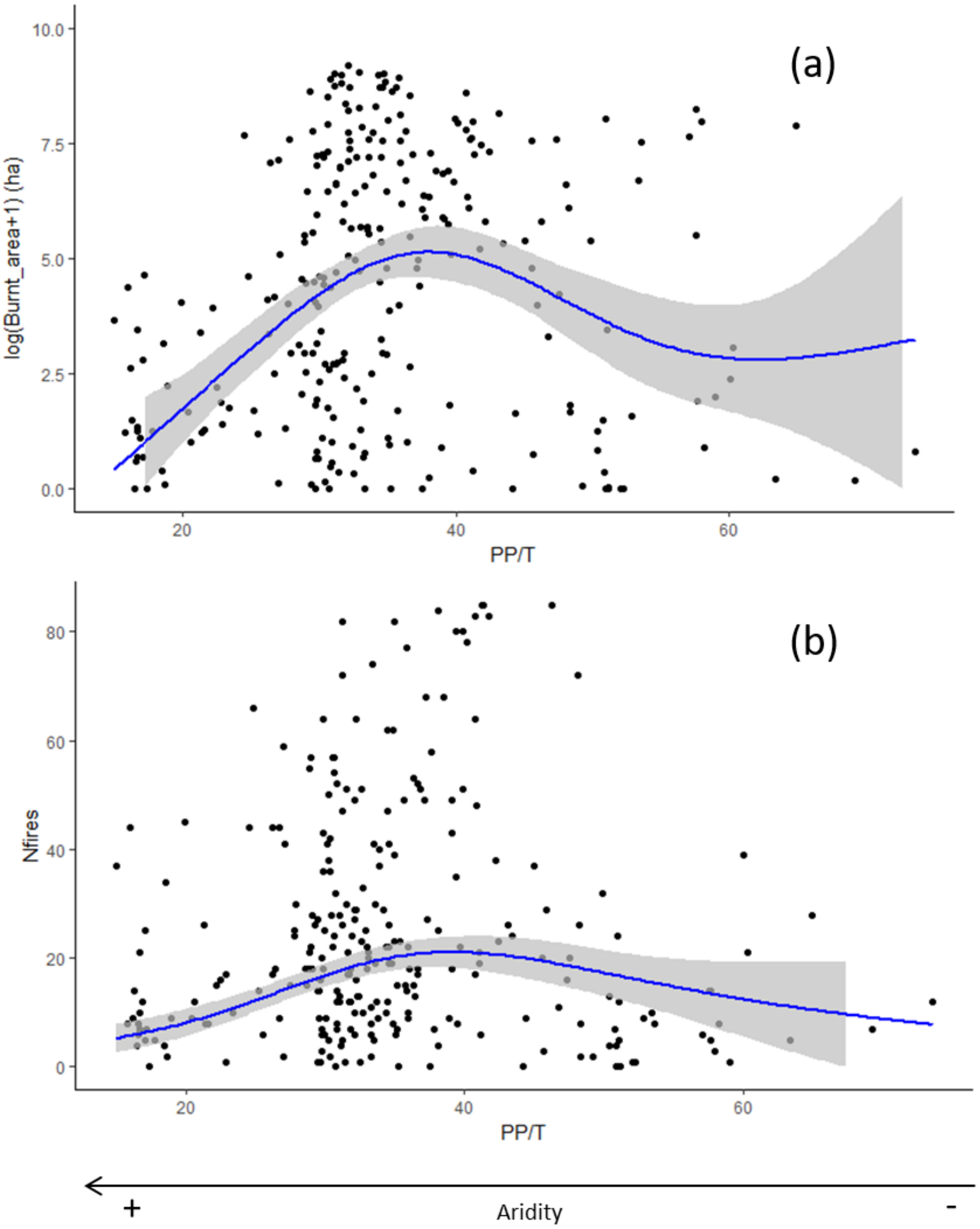

Figure 2. Relation of fire activity proxies with the climatic gradient (PP/T) for the Valencia Region; (a) total area burned; (b) number of fires for each 10×10 UTM coordinate. Blue lines and CI grey envelopes indicate the GAM models fitted for each proxy using the spatial data structure to correct spatial-autocorrelation (P<0.001). The climatic gradient is described as quotient PP/T (PP: mean annual precipitation, T: mean annual temperature).

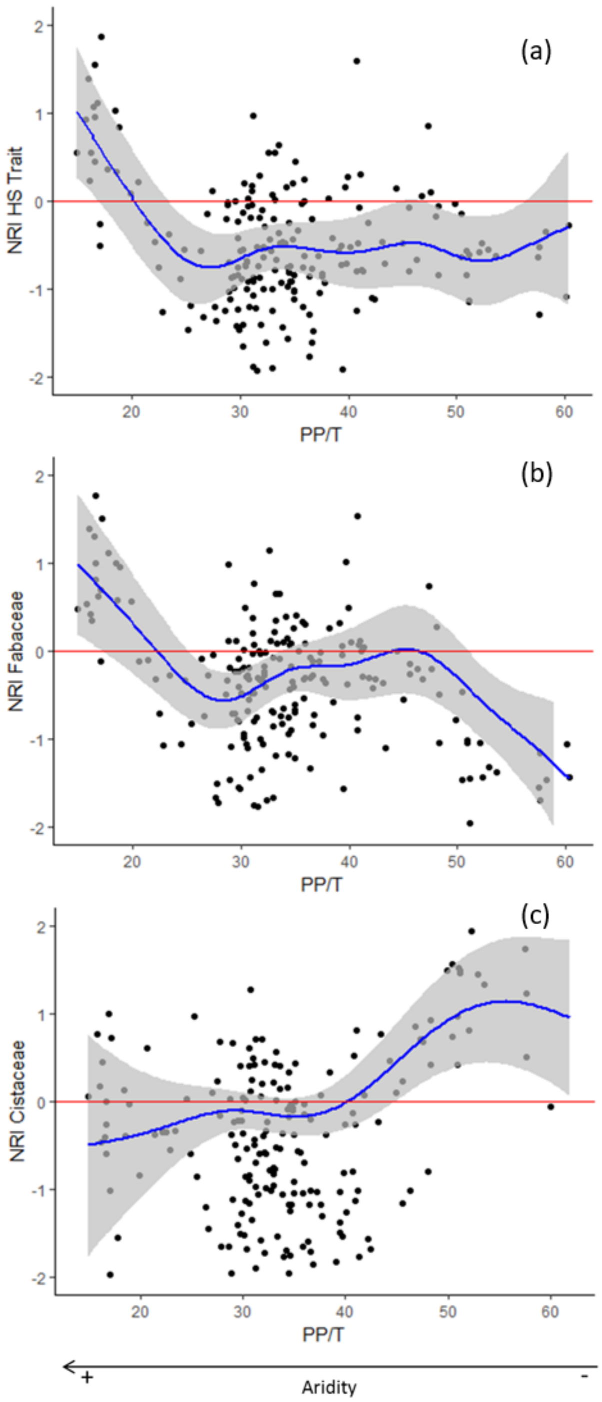

Figure 3. Net relatedness index (NRI) against the climatic gradient depicted in the Valencia Region (PP/T) for the Hardseededness trait (HS) (a) and the Fabaceae (b) and Cistaceae (c) families. Blue lines and CI grey envelopes indicate the GAM models fitted for each proxy using the spatial data structure to correct spatial-autocorrelation (P<0.001). The values above the red line indicate phylogenetic clustering, whereas those below it denote overdispersion. The

climatic gradient is described as quotient PP/T (PP: mean annual precipitation, T: mean annual temperature).

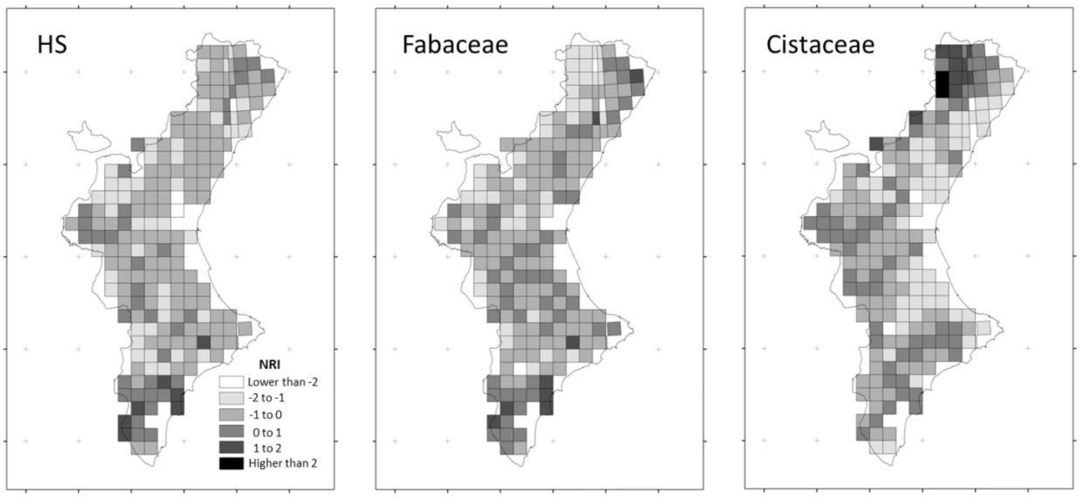

Figure 4. Spatial distribution in the Valencia Region of the Net Relatedness Index (NRI) for the Hardseededness trait (HS) and for the Fabaceae and Cistaceae families. Each square depicts a 10 ×10 UTM coordinate.