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Biological traits, habitat preferences and endemism in the flora of Peloponnisos, Greece

Abstract

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The Peloponnisos, the southernmost part of the Greek mainland, comprises 3,007 autochthonous spermatophytes (species and subspecies), including 4 Greek endemic genera. To compare biological traits within its flora, 4 main chorological categories were distinguished: widespread taxa, Greek endemics, range restricted taxa and local endemics. In the total flora, therophytes (34.8%) predominate, followed by hemicryptophytes (34.3%). A significant drop in the percentage of therophytes is noted among range restricted or local endemic taxa, with 11.6% and 1.3%, respectively. Diaspores are predominately seeds or single-seeded fruits, a trend even more pronounced in the range restricted and local endemic flora. Fleshy fruits are rare, with dry fruits being the norm in all categories. Annual seed production does not exhibit any significant variation among the widespread taxa and those having a restricted distribution. A preliminary investigation of dispersal syndromes showed that within genera specialized to particular dispersal modes the percentage of endemicity may vary considerably. Most Peloponnesian endemics inhabit rocky, calcareous habitats and cliffs. Dry, phryganic formations are also rich in endemics, followed by the grasslands at the lowland or subalpine areas. Ruderal and aquatic habitats have an insignificant contribution to endemism.

Key words: chorology, diaspore, dispersal, life forms, Mediterranean area.

Introduction

The range size of species and their distribution patterns on earth may vary considerably (Lamoreux & al. 2006). Endemism, as a term, refers to living organisms that have small ranges. It is usually a concept of spatial scale: endemic taxa are restricted to a defined geographic area or habitat (Gaston 2003; Hobohm 2014). Endemism is often associated with the political boundaries of countries or territories (e.g., islands, mountains) and when used in such a way, it is geographically defined.

Many endemic vascular plants have small populations and a limited geographical range. They face increased risk of area and/or population reduction and therefore, are inherently vulnerable to extinction. Very often, they are the targets of conservation efforts (Gaston

1998; Trigas & al. 2012; Keppel & al. 2018). Driving forces that shape endemism are certainly of importance, as they may be used in various models that predict endemism and/or decide on conservation priorities. Biological traits appear to have a major role in the ecological and evolutionary processes that diversify plant groups (Melendo & al. 2003; Balmford & Cowling 2006). The comparison of biological traits and ecological characteristics between local and widespread species could shed light on the driving forces that shape endemism and contribute to a better understanding of possible threats. This approach may also facilitate the application of appropriate conservation measures (Murray & al. 2002; Lavergne & al. 2004; Farnsworth 2007). Despite that acknowledgement, research on the plant traits that may contribute to a narrow spatial distribution remains limited (Bevill & Louda 1999; Casazza & al. 2005; Keppel & al. 2018). Currently, functional traits databases are emerging as an important tool for ecological studies. They can also be put in use for the identification of the relationships between plant characteristics and their relevant distribution patterns (Melendo & al. 2003; Díaz & al. 2016; Tavşanoğlu & Pausas 2018).

The Mediterranean Basin is one of the world's most important centers for plant diversity, due to its varied bioclimate, habitat heterogeneity and geologic history. Although representing only 1.6% of the Earth's surface, it hosts c. 10% of the world's higher plants (Médail & Quezél 1997). Southern and Central Greece has been identified as an important biodiversity hotspot within the Mediterranean basin (Médail & Quezél 1997, 1999). The region of Peloponnisos (Pe), at the southernmost part of the Greek mainland, hosts the highest number of endemic species and subspecies in Greece (Dimopoulos & al. 2013, 2016). Therefore, this region was selected as a model to investigate certain biological traits, particularly those related to dispersal and/or area occupation, life form and habitats within groups of different chorological characteristics.

The targets of this study include: a) the correlation of biological and habitat parameters within widespread and local plant taxa and b) a preliminary interpretation of our results as traits that are related to or promote endemism. To achieve the targets, the following steps have been taken: a) the floristic update of the vascular flora of Peloponnisos and the circumscription of different chorological groups that enable comparisons; b) the registration and identification of selected biological parameters that may reveal trait differences between widespread and local plants; c) the assignment of biological and habitat data to each species and subspecies.

Materials and methods

Study area

The study area includes the phytogeographical region of Peloponnisos (Pe) as defined in Strid & Tan (1997). It comprises Peloponnisos itself, i.e., the southernmost part of the Greek mainland, and several islands mostly to the east (Saronikos and Argolikos Gulfs islands) and to the south (Elafonisos, Kithira, Antikithira, Sapienza, Schiza). Two islets to the east (Velopoula and Falkonera) are remote and not included in the study area. The Corinth Canal, constructed in 1893, crosses the 6 km land belt that once formed the connection of Peloponnisos with adjacent Sterea Ellas and transformed the region into an artificial island. With a total surface area of approximately 22,140 km^2 (including surrounding

islands), Peloponnisos is certainly larger than Kriti (8,336 km^2) and comparable in size to Sicily (25,711km^2), the largest Mediterranean Island. Its highest elevation on Mt. Taigetos reaches 2,407 m (Fig. 1). Geologically, Peloponnisos is diverse with limestone, flysch and various sediment structures being the most important rock types. Annual precipitation varies from 400 to 1,700 mm, and the mean annual temperature ranges from 18.6°C in the warmest parts to 7.5°C on the highest peaks (see Trigas & al. 2012).

Flora and chorological categories

A number of literature and herbarium records were used to synthesize the total flora of Peloponnisos. As basic sources, Dimopoulos & al. (2013, 2016) were used to construct a floristic matrix that was later enriched by some recent bibliographic references. Important comments and additions to the flora of Peloponnisos are found in Strid & Tan (2017), Kalpoutzakis & al. (2019) and several contributions appearing in Phytologia Balcanica (Vladimirov & al. 2017a, 2017b, 2018a, 2018b, 2019) and Willdenowia (Raab-Straube & Raus 2017a, 2017b, 2018, 2019a, 2019b) journals. Most of the Greek endemic plants found in Peloponnisos are included in Tan & Iatrou (2001). Information from recent field work, particularly in the central parts of Peloponnisos, and the floristic databases maintained in ATH (c. 75,000 records) and ATHU (c. 33,000 records) were also used. As current investigation intends to reveal trends among widespread and local native taxa all records

Fig. 1. Peloponnisos (red square) covers the southernmost part of the Greek mainland. The highest peak of the region is on Mt. Taigetos (red dot; 2,407 m) (topographic background from Google Earth, google.com).

of alien, casuals and cultivated species were excluded from further analyses. Likewise, pteridophytes were not considered as they present different biological traits compared to spermatophytes.

We distinguish four main chorological categories: a) widespread taxa, i.e., plants that are distributed well beyond the political borders of Greece, b) Greek endemic taxa, i.e., species or subspecies confined within the political borders of Greece, c) range restricted taxa, i.e., taxa having an area of occurrence not exceeding a linear distance of 500 km irrespective of political borders and d) local endemics, i.e., taxa with a very narrow distribution, generally not exceeding a 50 km radius. The main matrix records the distribution of the above chorological categories in the total flora of Peloponnisos, the latter considered either with or without the surrounding islands.

Traits examined

Life-forms categories: The life-forms are according to the life-form system of Raunkiaer (1934) with subsequent extensions and amendments by Ellenberg & Mueller-Dobois (1967). As revealed during the process of our work, the hydrophytes and helophytes categories had a negligible contribution to endemism; therefore, they were both merged into the aquatic plant category. Life form abbreviations follow Dimopoulos & al. (2013) and make use of P for Phanerophytes, C for Chamaephytes, H for Hemicryptophytes, G for (non-aquatic) Geophytes, T for Therophytes and A for Aquatics. In cases that a taxon presents more than a single life form, the one of the mature plant (or best developed form) in Peloponnisos has been taken into consideration. If necessary, two life-forms per taxon were considered in our analyses.

Fruit type, type of diaspore and annual seed production: Fruits were classified as dry or fleshy, depending on whether a succulent layer of miscellaneous origin covers the seed/seed aggregate when ripe, or not. Fruits with a succulent hypanthium are considered fleshy. In the case of gymnosperms (no fruit present) the hard female cones of *Pinus*, *Abies* and *Cupressus* are considered dry, while the female cones of *Taxus*, *Juniperus* and *Ephedra* are considered fleshy. The diaspore may be a seed (or single seeded fruit such as an achene or a caryopsis) or a fruit (single or aggregated). Annual seed production refers to the average seed production per individual plant, per year (Tavşanoğlu & Pausas 2018). This can be estimated by knowing the number of ovaries per flower and the average number of flowers per plant, i.e., ignoring pollination or reproductive success. Four categories are recognized: no production (particularly in cases of vegetative propagation), few seeds ($\leq$ 50), several seeds (50-500) and many seeds ($>$ 500). For some taxa with a difficult estimation of annual seed production their herbarium specimens were consulted and in rare cases, some taxa were assigned to two categories and subject to separate analyses.

Pollination and dispersal modes: Pollination systems may be one or more for any given species. Following Faegri & Pijl (2016), taxa have been assigned to 4 main categories, i.e., anemogamous, entomogamous, autogamous or hydrogamous. For many plant taxa of Peloponnisos detailed knowledge on pollination syndromes is lacking. Flower morphology and the general instructions provided by Stebbins (1970) have been used to deduce main pollination syndrome.

Individual dispersal syndromes are those recognized by Tavşanoğlu & Pausas (2018) for the Mediterranean region. Literature records and access to BROT 2.0 (Tavşanoğlu &

Pausas 2018) and SID 7.1 (Royal Botanic Gardens Kew 2020) databases has been used for information extraction. In several cases, main dispersal mode for each taxon was decided by examining herbarium specimens in ATH and ATHU. Guidelines provided by Pijl (1982) and Bonn & al. (2000) were used for the assessment. Nine main dispersal syndromes are recognized: autochory (G), anemochory (W), hydrochory (H), ballistichory (B), myrmecochory (M), endozoochory (N), epizoochory (E), hoarding by animals (O), and zoochory (Z) for dispersal mediated by animals in an unknown way. Attributing a main dispersal mode to the whole Peloponnisos flora (more than 3,000 taxa) left several unresolved cases that currently do not permit handling of the dataset as a whole. However, pollination and dispersal modes have been used in particular taxonomic groups to trace tendencies among endemic and widespread taxa categories.

Habitats: Two different approaches were used: a) habitat preference for each taxon according to Dimopoulos & al. (2013). The categories have as follows: freshwater aquatic habitats (A); cliffs, rock faces and walls (C); temperate and Mediterranean grasslands (G); above treeline vegetation on high mountains (H); marine and coastal habitats influenced by salt (M); xeric Mediterranean phrygana and grasslands (P); agricultural and ruderal habitats (R); woodland and scrub (W). When a taxon is found in more than one habitats, different analyses took into consideration its predominant habitat, or its more than one recorded habitats. b) Habitat preference according to the European EUNIS habitat types at various levels (downloaded from: https://www.eea.europa.eu/data-and-maps/data/eunis-habitat-classification). In this latter approach important information had to be retrieved from the literature and also, from specimen labels maintained in ATH and ATHU herbaria and databases. Still, some gaps in knowledge do not permit a direct analysis of the whole set of results, at present.

Results

Peloponnisos comprises 3,007 autochthonous spermatophyte taxa (species and subspecies, see Electronic Supplementary file 1), which constitute almost half of the Greek flora. This number does not include aliens or cultivated plants escaped from man-made habitats and pteridophytes that differ from spermatophytes in important biological aspects. We recorded 475 taxa as Greek endemics, including 4 Greek endemic genera: *Hymenonema* (see Liveri & al. 2018), *Laserocarpum* (Spalik & al. 2019), *Thamnosciadium* and *Phitosia* (Fig. 2). The latter, *Phitosia*, is the only genus exclusively endemic to Peloponnisos and distributed on two mountains to the south: Taigetos and Parnonas (Kamari & al. 2010). The number of range restricted taxa present in the flora of Peloponnisos is 518, higher by 43 taxa from the number of Greek endemics. The number of local endemics is also notable: 77 taxa have a very narrow distribution that does not exceed a linear distance of c. 50 km.

The richest families in Greek endemic, range restricted, and local endemic taxa of the Peloponnesian flora are somewhat irregularly distributed among the total flora. In decreasing order, high numbers are found in *Asteraceae* (83, 92 and 14 taxa, respectively), *Caryophyllaceae* (55, 62, 6), *Lamiaceae* (39, 42, 6), *Brassicaceae* (23, 26, 3) and *Rubiaceae* (22, 23, 3). *Asteraceae* and *Caryophyllaceae* have the highest number of taxa

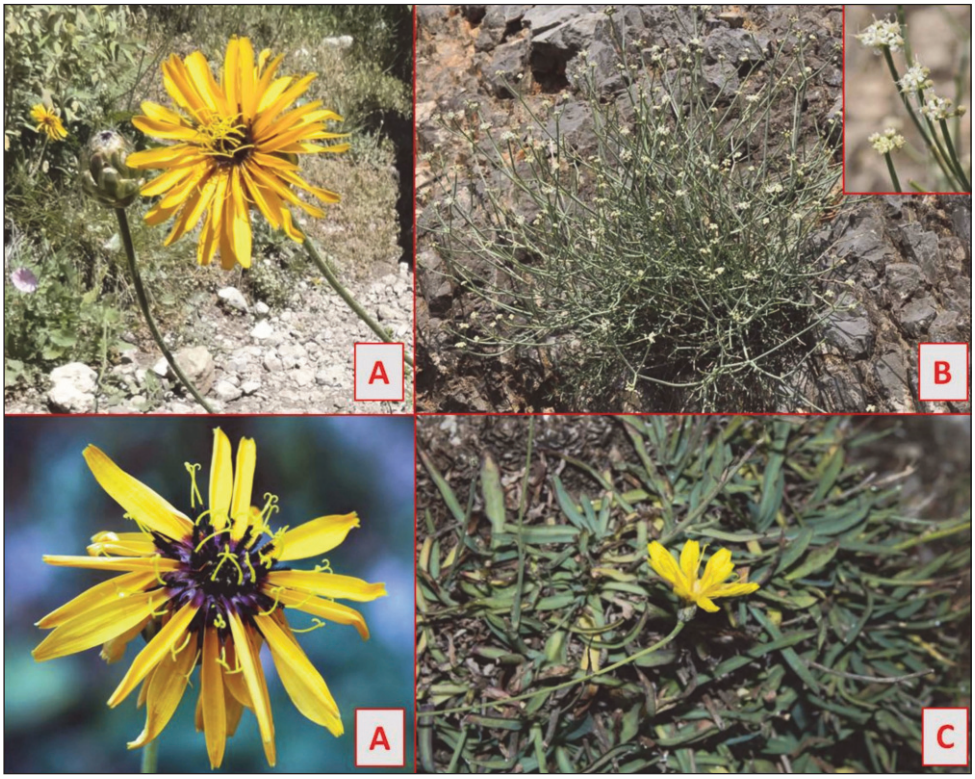

Fig. 2. Three endemic genera in the flora of Peloponnisos: A, *Hymenonema* with *H. laconicum* Boiss. & Heldr.; B, *Thamnosciadium* with *Th. junceum* (Sm.) Hartvig, monotypic; C, *Phitosia* with *Ph. crocifolia* (Boiss. & Heldr.) Kamari & Greuter, monotypic.

in all categories and are among the most species-rich families of the Greek flora. *Poaceae*, the second richest family of the Greek flora, presents rather low numbers of Greek endemic, range restricted and local endemic taxa (11, 13, 1, respectively).

An analysis of the life form categories reveals some noteworthy results (Fig. 3). In the widespread flora, the therophyte category predominates with 989 taxa being annuals or chiefly annuals (39.7%), followed by the hemicryptophytes (31.4%, 781 taxa) and the geophytes (13.1 %, 326 taxa). The lowermost percentage (1.7%) is attributed to the aquatic plants, with 42 taxa. In the endemic and range restricted categories, the percentages change remarkably, compared to the widespread taxa. Here, the percentage of therophytes drops to 10.8% (for the range restricted category) and the percentage of hemicryptophytes rises to 54.6%. Geophytes remain, correspondingly, almost unaltered (14.5% in the range restricted category). The chamaephyte percentage increases by 3 times (18.4%) and the aquatic plants nullify. Changes become even more dramatic among the local endemics with only one therophyte (1.3%), 46 hemicryptophytes (59.8%), 18 chamaephytes (23.4%) and 10 geophytes (13.0%). Two taxa are phanerophytes (2.6%).

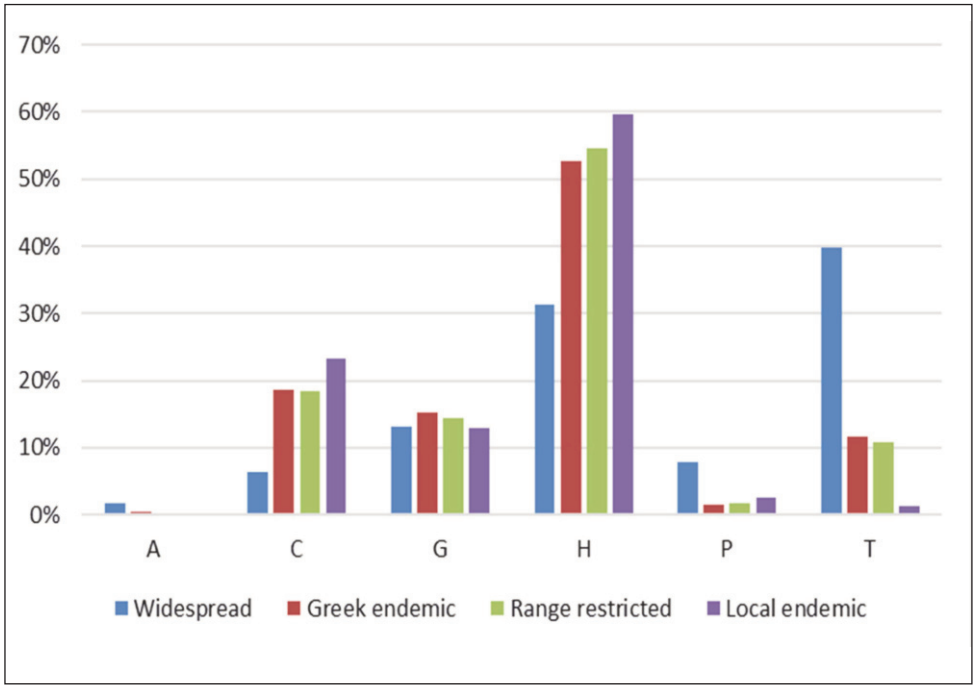

Fig. 3. Percentage of life form groups in each of the four chorological categories of the Peloponnisos flora. The abbreviations mean aquatic plants (A), chamaephytes (C), geophytes (G), hemicryptophytes (H), phanerophytes (P), and therophytes (T). Therophytes predominate in the widespread taxa (39.7%) but their percentage diminishes in the Greek endemic (11.6%), range restricted (10.8%), and especially local endemic (1.3%) categories, where the dominant life form are the hemicryptophytes (52.7%, 54.5% and 59.7% respectively).

The fruit type is an important character and may affect dispersal modes and distances. In the flora of Peloponnisos, the fleshy fruit type is rare, accounting for 6.2% among the widespread taxa, 1.3% among the Greek endemics and 1.2% among the range restricted taxa. Within local endemics, the percentage is remarkably similar to that of the Greek endemics and the range restricted taxa, and remains stable to 1.3%. As a consequence of the above, the dry fruit types are widespread in all life form categories and certainly dominant within the endemic, range restricted and local endemic categories.

The diaspore categories were examined somewhat complementary to the fruit type and the number of annual seed production. The two categories, i.e., a seed or a dry/monospermous fruit vs. a single or an aggregate fruit (polyspermous, as a rule) were evaluated in all chorological categories. The seed characterizes 1671 taxa of the widespread flora (67.6%) and the fruit 802 (32.4%). These percentages shift towards the seed category in the Greek endemic (83.5%), range restricted (84.9%), and local endemic (84.4%) chorological groups (Fig. 4). That means that the seed diaspore is approximately 5 times more common than the fruit among the chorologically restricted taxa vs. 2 times more common than the fruit among the widespread taxa.

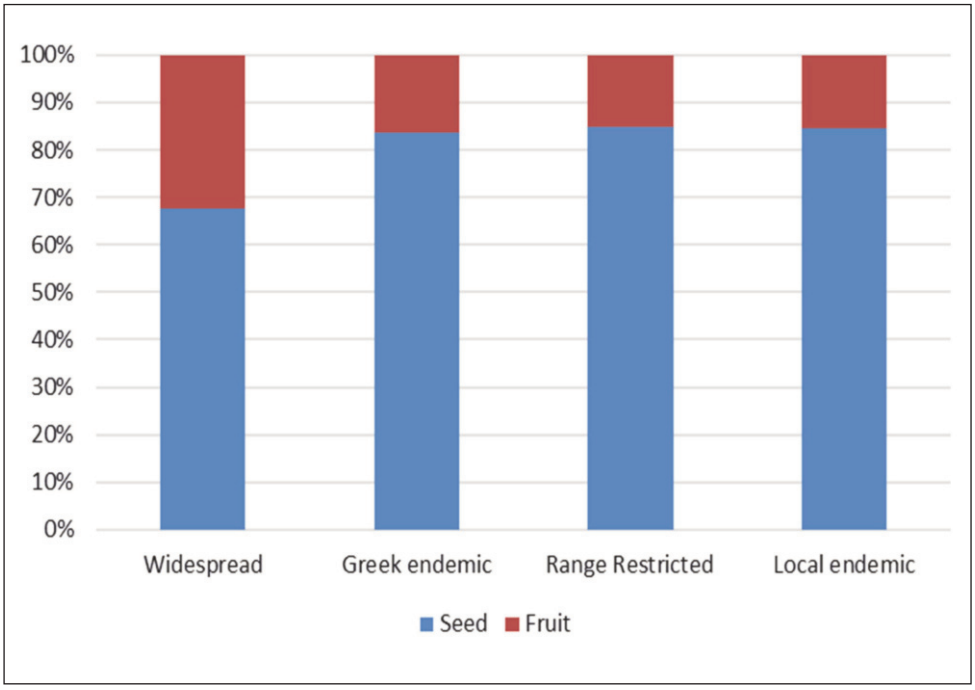

Fig. 4. The seed is the most common diaspore in the flora of Peloponnisos. The percentage of taxa developing and releasing a seed-type diaspore is 67.6% among the widespread taxa and between 83.5 to 84.9% in the Greek endemic, range restricted and local endemic categories.

Annual seed production was evaluated for practically all the taxa of Peloponnisos, yet we are aware that this parameter may, at least partly, be influenced by climate oscillations, soil fertility and plant development, during any period of years. Our estimations show that annual seed production percentages do not vary much among the widespread and the restricted taxa. The widespread taxa produce few (16.0%), a medium quantity (65.9%) and many (18.1%) seeds. Within the taxa of limited distribution the percentages are 18.0%-24.7% for the few seed category, 59.7%-62.1% for the medium quantity and 15.6%-19.9% for the many seed category.

Pollination and dispersal modes have been used rather selectively, in a few analyses at present. Information on plants dispersal modes for the flora of Peloponnisos is scarce and presumably not always trustworthy. Some preliminary experiments with *Biarum* sp. (a geophyte) and *Centaurea sonchifolia* L. (a hemicryptophyte) in cultivation indicate the presence of two dispersal modes in each taxon (a dual dispersal pattern, diplochory, e.g., autochory and myrmecochory, autochory and hydrochory, see Vander Wall & Longland (2004). In the case of *C. sonchifolia* the presence of a fruit appendage (a pappus, indicative of anemochory) is counteracted by the fruit mass. These heavy fruits present autochory rather than anemochory but other secondary dispersal mechanisms are also possible (Der Weduwen & Ruxton 2019). Likewise, we observed autochory and possible myrmecochory

in *Biarum*. In this latter case, the estimation of seed dispersal distances (see Vittoz & Engler 2007) as revealed by the emergence of new seedlings over a period of three years varies from 8 to 190 cm.

In order to correlate chorology with a particular dispersal mode we have selected myrmecochory in three unrelated genera that possess an elaiosome in their seed (see Gorb & Gorb 2003): *Crocus, Euphorbia* and *Viola.* Numbers of taxa and distribution of chorological categories appear to be random, with *Crocus* and *Viola* (but not *Euphorbia*) comprising several Greek or local endemics (Fig. 5).

Habitats in relation to the four chorological categories appear in Fig. 6. Grasslands, ruderal habitats and phrygana comprise the highest numbers of widespread taxa in the flora of Peloponnisos. In the Greek endemic and range restricted categories the cliffs, grasslands and phrygana habitats harbour most of the endemics, with the ruderal habitats contributing in lower numbers. Among local endemics, the highest number of taxa is found in cliff habitats, with phrygana and above treeline habitats on mountains contributing with smaller taxa numbers. Interestingly, aquatic habitats have a zero number of local endemics, while ruderal habitats have a small contribution, both among the range restricted and the local endemics but not among taxa of the widespread category, where their contribution is considerable. Fig. 6 depicts the percentages of habitat contributions to the four chorological

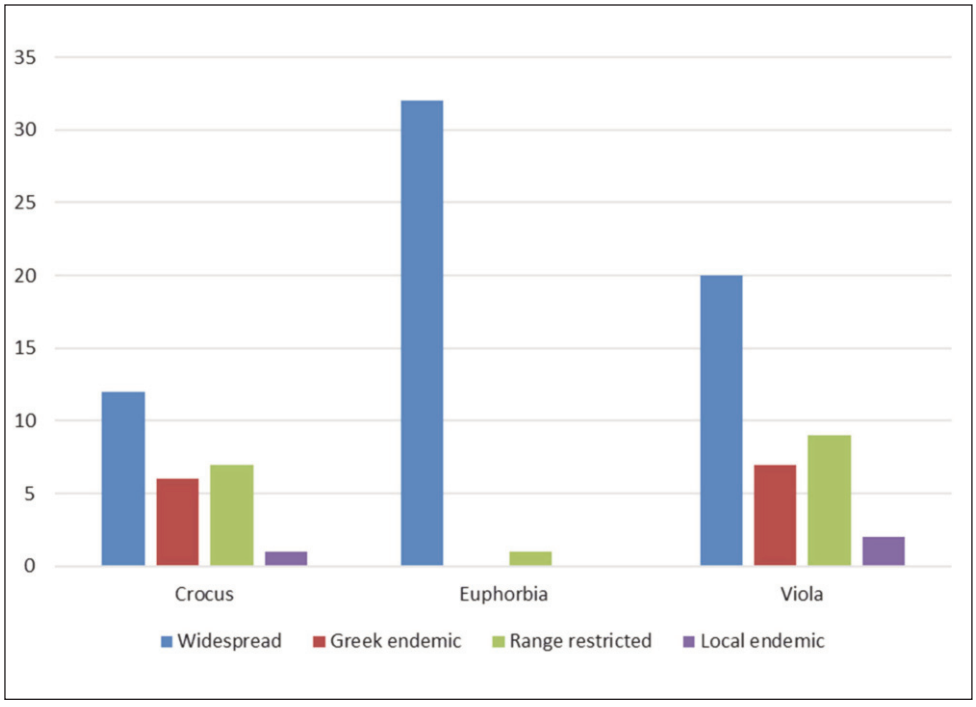

Fig. 5. The numbers of widespread, Greek endemic, range restricted, and local endemic taxa in three random entomophilous and myrmecochorous genera of Peloponnisos (*Crocus*, *Euphorbia*, *Viola*) vary considerably.

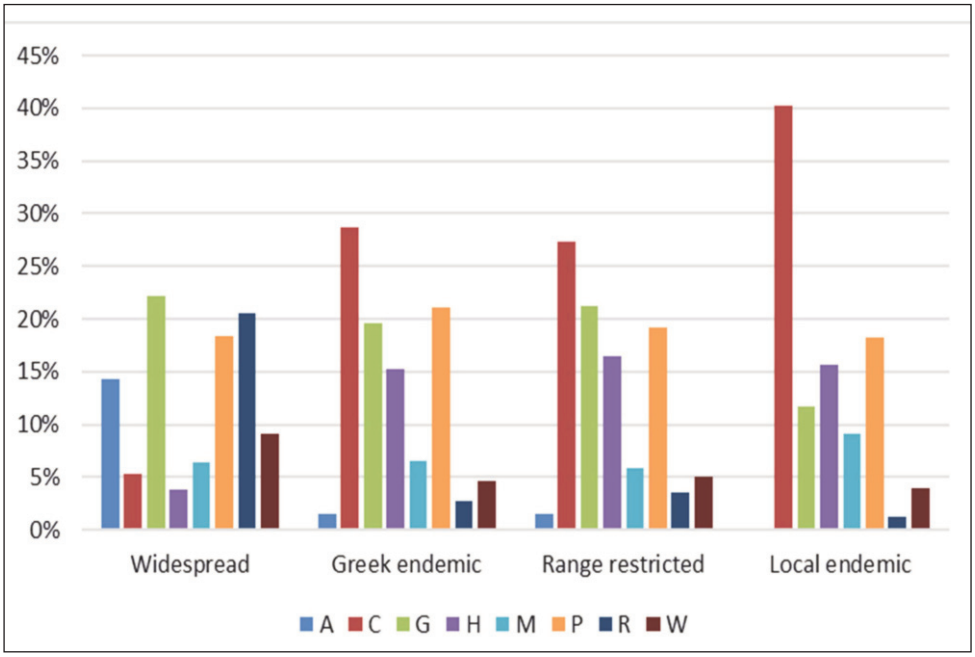

Fig. 6. Shifts in habitats appear in this comparative presentation for members of the four chorological categories. Notice the significant percentage changes in aquatic (A, 0.0% to 14.3%), cliffs and rocks (C, 5.3% to 40.3%) and ruderal (R, 1.3% to 20.6%) habitats as opposite to the relative stability of the coastal (M, 6.3% to 9.1%) and phrygana (P, 18.2% to 21.1%) habitats. For the abbreviations see also under Habitats in Materials and Methods.

categories. Note the shifts of the cliff and rock habitat (small contribution in the widespread, large or very large in the remaining chorological categories) and the aquatic habitat, as indicated above. In contrast, the phrygana and the coastal habitats have a rather stable contribution in all four groups.

Discussion and conclusions

Endemism and the factors that drive particular plant species to exhibit narrow distribution areas have been studied using various approaches. Environmental factors (e.g., altitude, geological substrate, rainfall, anthropogenic disturbance) have been usually analyzed to comprehend the ecological behavior and the present-day distribution patterns of endemic plants in the Mediterranean (Casazza & al. 2005; Trigas & al. 2013; Tomović & al. 2014; Fois & al. 2017). The necessity to understand biological and ecological factors that interfere with the distribution and maintenance of endemic plant taxa is currently even more pronounced since many of them are threatened and in need of conservation actions.

The endemic spermatophyte flora of Peloponnisos has been estimated here at three different levels: the Greek endemic flora (border-dependent) accounts for 15.8% of the total, the range restricted flora (border-independent) accounts for 17.2%, and the very localized endemic flora for 2.6%. Given the dynamic nature of the alien flora and its dissociation with endemism, all its Peloponnesian members have been excluded from analyses. An evaluation and comparison of life form patterns among the three endemic plant categories versus the widespread flora reveals a significant deviation from the norm: therophytes in all endemic chorological categories contribute to the life form spectra significantly less than the expected c. 25-50% found in the Mediterranean region. Local endemics exhibit the lowermost percentage. Low levels of annual taxa contribution to the endemicity assemblage has also been observed in the whole Greek flora (Dimopoulos & al. 2013) and in other Mediterranean countries as well (Amich & al. 2004; Giménez & al. 2004). Interpretations of this low percentage take into account the habitat preferences and the rainfall gradient of habitats where endemic taxa predominate: rocky environments and cliffs present a low percentage of therophytes but a high number of endemics (Panitsa & Kontopanou 2017; this study). Presumably, the weak root system of therophytes does not enable them withstand wind blowdowns and/or reach available water resources under the extreme conditions prevailing on cliffs (see Georghiou & Delipetrou 2010). An increased percentage of endemic plants at the above-treeline habitats on high mountains is correlated with increased precipitation levels and lower selection pressures to adopt an annual life form. In the south of Spain, therophytes, as opposite to hemicryptophytes, exhibit an inverse altitudinal distribution pattern: their rate tends to decrease as altitude increases. They present a clear positive correlation with the thermomediterranean belt and a negative correlation with the oromediterranean belt (Giménez & al. 2004). An investigation in Israel points to an optimum between 200 and 500 mm average mean annual rainfall for therophytes (Danin & Orshan 1990). For the same reasons (i.e., rocky habitat specialization, above treeline areas colonization with high precipitation, robust root system), the percentage of hemicryptophytes and chamaephytes among Mediterranean endemic plants is generally high (see also Vuksanović & al. 2016 for a study in Montenegro).

As a rule, plants of Peloponnisos do not produce fleshy fruits and this is even more pronounced in its endemic flora. Fleshy fruits are correlated to frugivory, i.e., fruit consumption by birds and mammals, which later on act as the major vertebrate seed dispersers in most terrestrial habitats (endozoochory). The very low percentage of fleshy fruit production among the endemic plants of Peloponnisos (1.2-1.3% versus 6.2% among the widespread category) may be an indication of low evolutionary mutualisms between endozoochorous plants and seed dispersers. The frugivorous animals that do exist in Peloponnisos may contribute in a general, unspecialized manner to fruit dispersal and endemic plants are less adapted to such a syndrome. This combines well with the main diaspore unit, which is the seed (or dry monospermous fruit), not the fruit, among the endemic categories. Furthermore, fleshy fruits are mostly produced in families of woody plants; families that are primarily herbaceous produce capsular or other kinds of dry fruits (Fleming & Kress 2011). Phanerophytes that exhibit fleshy fruits are rare among each chorological group of the endemics, with only a few taxa, 2 to 9, belonging to this life form category. Moreover, it appears that the Mediterranean fruit-bearing plants did not evolve any particular mutualistic behavior to benefit from animal dispersers. According to Herrera (1995), with

respect to birds, variation in fruiting phenology, fruit shape, nutritional composition of fruits, and structural fruit characteristics in Mediterranean plants are more closely tied to phylogeny or to the abiotic environment than to the current disperser/dispersal prerequisites. Such a lack of disperser/dispersal specificity is apparently maintained among the endemic plants of Peloponnisos.

A comparison of annual seed production did not reveal any noteworthy differences among widespread taxa and any of the chorologically restricted groups, at the scale level examined. Number of seeds produced, per plant per year, can perhaps affect population size, particularly in annual plants that spend considerable time as dormant propagules in edaphic seedbanks. Seed mass, on the other hand, may have a critical role in dispersal distances and population expansion. Our collected data on seed mass is preliminary and does not allow comparison between widespread and local taxa, at present. Nevertheless, experiments by Lavergne & al. (2003) in southern France conducted across 13 pairs of rock endemic species and widespread congeners failed to show any statistically significant difference in seed mass between the two groups.

Pollination and particularly dispersal modes have been the most challenging biological traits we examined in this study. Soon after realizing the low number of studies on dispersal traits in Greek plants, we came across a number of parameters we had to assess in the field and in the laboratory and often combine, in order to decide on dispersal strategies. As we currently understand and despite maintaining the basic dispersal categories of Tavşanoğlu & Pausas (2018), things appear to be more complicate in nature. Hintze & al. (2013) developed the D^3, the Dispersal and Diaspore Database (to which we had no access), to quantify rather than qualify the adaptation to dispersal modes for any given taxon. Our first approaches using simple morphological characters of seed (shown in Fig. 5) or fruit (anemochory vs. barychory vs. zoochory in *Apiaceae*, not shown) failed to reveal differences among widespread and local taxa in their dispersal modes. Still, we feel that more than one parameters have to be added to simple histograms like the one of Fig. 5, before deciding about their usefulness in revealing traits. For example, the addition of seed mass would be a critical and decisive character for Fig. 5, in case that data were available for all the Peloponnesian members of the three genera. Interestingly, Gabrielová & al. (2013) found differences between Critically Endangered taxa (CR - many highly threatened species are local endemics in Greece) and common species in their mode of dispersal, in the Czech Republic. According to their results, epizoochory and hydrochory dispersal modes had a significantly higher proportion, while endozoochory and hemerochory a lower proportion, in the CR species, when compared to common species.

Finally, different habitats have been analyzed in relation to different chorological categories and important traits have been observed in this study. Most plants in the endemic categories grow on cliffs and rocky slopes, ravines and walls. For local endemics, the percentage of taxa behaving as cliff dwellers reaches 40.3%. Apart from the shift in life forms, which is partly correlated with rocky habitats, the endemic taxa clearly prefer habitats with a higher percentage of bedrock and block cover and grow on significantly steeper slopes than their widespread congeners. Cliffs and rocky places in the Mediterranean generally have a lower cover of herbaceous and woody species, a smaller number of coexisting species, and a significantly lower vegetation canopy height than habitats of widespread species (Thomson & al. 2005; observations in the western Mediterranean). The cliffs and

rocks environment is also related to plant competition, which may be less intense in rocky habitats, and a refugium role, present in many rock systems and cliffs in Greece and the Mediterranean (e.g., Kypriotakis & Tzanoudakis 2001). Important parameters of the chasmophytic Greek flora are presented by Panitsa & Kontopanou (2017). The second important habitat, phrygana and xeric land, has an almost similar proportion among widespread taxa and the three categories of endemic taxa. The third most important habitat, high-mountain vegetation, is related to the isolation found on the above treeline areas on high mountains and its contribution is significant in the endemic categories. The way elevation gradient shapes endemism in Kriti Island, just south of Peloponnisos, is presented by Trigas & al. (2013).

The most important conclusions of this study focused on biological traits, habitat preferences and endemism in the flora of Peloponnisos are the following: a) groups of narrow distributed taxa have different life form spectra compared to widespread taxa or the total flora. Hemicryptophytes and chamaephytes prevail among endemics, whereas therophytes contribute with low percentages; b) fleshy fruits are very rare among the endemic categories and contribute to an even lower percentage as plant diaspores, compared to widespread taxa; c) annual seed production is rather similar, among widespread and narrowly distributed taxa; d) dispersal modes are complicate and need further study. Several different parameters should be evaluated and analyzed, before safe conclusions regarding widespread and local taxa are reached; e) habitat shifts are observed among endemics and local endemics, compared to widespread taxa. More than 40% of the local endemic flora behaves as rock and cliff dwellers, a fact that stresses the importance of these habitats as conservation targets.

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References

Amich, F., Bernardos, S., Aguiar, C., Fernández-Diez, J. & Crespí, A. 2004: Taxonomic composition and ecological characteristics of the endemic flora of the lower Duero Basin (Iberian Peninsula). – Acta Bot. Gall. **151(4):** 341-352. https://doi.org/10.1080/12538078.2004.10515439

Balmford, A. & Cowling, R. M. 2006: Fusion or failure? The future of conservation biology. – Conserv. Biol. **20(3):** 692-695. https://doi.org/10.1111/j.1523-1739.2006.00434.x

Bevill, R. L. & Louda, S.M. 1999: Comparisons of related rare and common species in the study of plant rarity. – Conserv. Biol. **13(3):** 493-498. https://doi.org/10.1046/j.1523-1739.1999.97369.x

Bonn, S., Poschlod, P. & Tackenberg, O. 2000: Diasporus – a database for diaspore dispersal-concept and applications in case studies for risk assessment. – Z. Ökol. Umweltschutz **9:** 85-97.

Casazza, G., Barberis, G. & Minuto, L. 2005: Ecological characteristics and rarity of endemic plants of the Italian Maritime Alps. – Biol. Conserv. **123(3):** 361-367.

Danin, A. & Orshan, G. 1990: The distribution of Raunkiaer life forms in Israel in relation to the environment. – J. Veg. Sci. **1:** 41-48. https://doi.org/10.1016/j.biocon.2004.12.005

Der Weduwen, D. & Ruxton, G. D. 2019: Secondary dispersal mechanisms of winged seeds: a review. – Biol. Rev. **94(5):** 1-9. https://doi.org/10.1111/brv.12537

Díaz, S., Kattge, J., Johannes Cornelissen, H. C. J., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I. C., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., Chave, J., Wright, S. J., Seremet'ev, S. N., Jactel, H., Baraloto C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J. S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M. D. & Gorné, L. D. 2016: The global spectrum of plant form and function. – Nature **529:** 167-171. https://doi.org/10.1038/nature16489

Dimopoulos, P., Raus, Th., Bergmeier, E., Constantinidis, Th., Iatrou, G., Kokkini, S., Strid, A. & Tzanoudakis, D. 2013: Vascular plants of Greece: an annotated checklist. – Englera **31.**

—, —, —, —, —, —, — & — 2016: Vascular plants of Greece: an annotated checklist. Supplement. – Willdenowia **46:** 301-347.

Ellenberg, H. & Mueller-Dombois, D. 1967: A key to Raunkiar plant life forms with revised subdivisions. – Ber. Geob. Inst. ETH Rübel, Zürich **37:** 56-73.

Faegri, K. & Pijl van der, L. 2016: Principles of pollination ecology. – Oxford.

Farnsworth, E. J. 2007: Plant life history traits of rare versus frequent plant taxa of sandplains: implications for research and management trials. – Biol. Conserv. **136(1):** 44-52. https://doi.org/10.1016/j.biocon.2006.10.045

Fleming, T. H. & Kress, W. J. 2011: A brief history of fruits and frugivores. – Acta Oecol. **37:** 521-530. https://doi.org/10.1016/j.actao.2011.01.016

Fois, M., Fenu, G., Cañadas, E. M. & Bacchetta, G. 2017: Disentangling the influence of environmental and anthropogenic factors on the distribution of endemic vascular plants in Sardinia. – PLoS ONE **12(8):** e0182539. https://doi.org/10.1371/journal.pone.0182539

Gabrielová, J., Münzbergová, Z., Tackenberg, O. & Chrtek, J. 2013: Can we distinguish plant species that are rare and endangered from other plants using their biological traits? – Folia Geobot. **48:** 449-466. https://doi.org/10.1007/s12224-012-9145-x

Gaston, K. J. 1998: Rarity as double jeopardy. – Nature **394:** 229-230. https://doi.org/10.1038/28288

— 2003: The structure and dynamics of geographic ranges. – New York.

Georghiou, K. & Delipetrou, P. 2010: Patterns and traits of the endemic plants of Greece. – Bot. J. Linn. Soc. **162(2):** 130-153. https://doi.org/10.1111/j.1095-8339.2010.01025.x

Giménez, E., Melendo, M., Valle, F., Gómez-Mercado F. & Cano, E. 2004: Endemic flora biodiversity in the south of the Iberian Peninsula: altitudinal distribution, life forms and dispersal modes. – Biodivers. Conserv. **13:** 2641-2660. https://doi.org/10.1007/s10531-004-2140-7

Gorb, E. & Gorb, S. (eds) 2003: Seed dispersal by ants in a deciduous forest ecosystem – Dordrecht.

Herrera, C. M. 1995: Plant-vertebrate seed dispersal systems in the Mediterranean - ecological, evolutionary, and historical determinants. – Ann. Rev. Ecol. Syst. **26:** 705-727. https://doi.org/10.1146/annurev.es.26.110195.003421

Hintze, C., Heydelb, F., Hoppe, C., Cunzea, S., König, A. & Tackenberg, O. 2013: D^3: The dispersal and diaspore database – baseline data and statistics on seed dispersal. – Perspect. Pl. Ecol. Evol. Syst. **15:** 180-192. https://doi.org/10.1016/j.ppees.2013.02.001

Hobohm, C. (ed.) 2014: Endemism in vascular plants. – Dordrecht, Heidelberg, New York & London.

Kalpoutzakis, E., Constantinidis, Th., Trigas, P. 2019: Chorological additions for some noteworthy taxa of the Greek flora. – Bot. Chron. **22:** 233-249.

Kamari, G., Kyriakopoulos, C. & Kofinas, C. 2010: New finding of *Phitosia crocifolia* (*Compositae*) in E Peloponnisos. – Fl. Medit. **20:** 235-238.

Keppel, G., Ottaviani, G., Harrison, S. Wardell-Johnson, G. W., Marcantonio M. & Mucina, L. 2018: Towards an eco-evolutionary understanding of endemism hotspots and refugia. – Ann. Bot. **122(6):** 927-934. https://doi.org/10.1093/aob/mcy173

Kypriotakis, Z. & Tzanoudakis, D. 2001: Contribution to the study of the Greek insular flora: the chasmophytic flora of Crete. – Bocconea **13:** 495-503.

Lamoreux, J. F., Morrison, J. C., Ricketts, T. H., Olson, D. M., Dinerstein, E., McKnight, M. W. & Shugart, H. H. 2006. Global tests of biodiversity concordance and the importance of endemism. – Nature **440:** 212-14. https://doi.org/10.1038/nature04291

Lavergne, S., Garnier, E. & Debussche, M. 2003: Do rock endemic and widespread plant species differ under the leaf-height-seed plant ecology strategy scheme? – Ecol. Lett. **6:** 398-404. https://doi.org/10.1046/j.1461-0248.2003.00456.x

—, Thompson, J. D., Garnier, E. & Debussche, M. 2004: The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. – Oikos **107(3):** 505-518. https://doi.org/10.1111/j.0030-1299.2004.13423.x

Liveri, E., Bareka, P. & Kamari, G. 2018: Taxonomic study on the Greek endemic genus *Hymenonema* (*Asteraceae*: *Cichorieae*), using morphological and karyological traits. – Willdenowia **48:** 5-21. https://doi.org/10.3372/wi.48.48101

Médail, F. & Quezél, P. 1997: Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. – Ann. Missouri Bot. Gard. **84(1):** 112-127. https://doi.org/10.2307/2399957

— & — 1999: Biodiversity hotspots in the Mediterranean Basin: setting global conservation priorities. – Conserv. Biol. **13(6):** 1510-1513. https://doi.org/10.1046/j.1523-1739.1999.98467.x

Melendo, M., Giménez, E., Cano, E., Gómez-Mercado, F. & Valle, F. 2003: The endemic flora in the south of the Iberian Peninsula: taxonomic composition, biological spectrum, pollination, reproductive mode and dispersal. – Flora **198:** 260-276. https://doi.org/10.1078/0367-2530-00099

Murray, B. P., Thrall, P. H., Gill, A. M. & Nicotra, A. B. 2002: How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. – Austral. Ecol. **27(3):** 291-310. https://doi.org/10.1046/j.1442-9993.2002.01181.x

Panitsa, M. & Kontopanou, A. 2017: Diversity of chasmophytes in the vascular flora of Greece: floristic analysis and phytogeographical patterns. – Bot. Serb. **41(2):** 199-211.

Pijl van der, L. 1982: Principles of dispersal in higher plants. – Berlin & Heidelberg.

Raab-Straube E. von & Raus Th. (eds) 2017a: Euro Med-Checklist Notulae, 7 – Willdenowia **47(1):** 89-96.

— & — (eds) 2017b: Euro Med-Checklist Notulae, 8. – Willdenowia **47(3):** 293-309.

— & — (eds) 2018: Euro Med-Checklist Notulae, 9. – Willdenowia **48(2):** 195-220.

— & — (eds) 2019a: Euro Med-Checklist Notulae, 10. – Willdenowia **49(1):** 95-115.

— & — (eds) 2019b: Euro Med-Checklist Notulae, 11. – Willdenowia **49(3):** 421-445.

Raunkiaer, C. 1934: The life forms of plants and statistical plant geography. – Oxford.

Royal Botanic Gardens Kew. (2020) Seed Information Database (SID). Version 7.1. Available from: http://data.kew.org/sid/ (February 2020)

Spalik, K., Wojewódzka, A., Constantinidis, Th., Downie, S. R., Gierek, M. & Banasiak, Ł. 2019: *Laserocarpum*, a new genus of *Apiaceae* endemic to Greece. – Acta Soc. Bot. Pol. **88(3):** 3635. https://doi.org/10.5586/asbp.3635

Stebbins, G. L. 1970: Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. – Ann. Rev. Ecol. Syst. **1(1):** 307-326. https://doi.org/10.1146/annurev.es.01.110170.001515

Strid, A. & Tan, K. (eds) 1997: Flora hellenica, **1.** – Konigstein

— & — 2017: Recent progress in plant taxonomy and floristic studies in Greece. – Bot. Serbica **41(2):** 123-152.

Tan, K. & Iatrou, G. 2001: Endemic plants of Greece - the Peloponnese. – Copenhagen.

Tavşanoğlu, C. & Pausas, J. 2018: A functional trait database for Mediterranean Basin plants. – Sci. Data **5:** 180135. https://doi.org/10.1038/sdata.2018.135

Thomson, J. D., Lavergne, S., Affre, L., Gaudeu, M., & Debussche1, M. 2005: Ecological differentiation of Mediterranean endemic plants. – Taxon **54(4):** 967-976. https://doi.org/10.2307/25065481

Tomović, G., Niketić, M., Lakušić, D., Ranđelović, V. & Stevanović, V. 2014: Balkan endemic plants in Central Serbia and Kosovo regions: distribution patterns, ecological characteristics, and centres of diversity. – Bot. J. Linn. Soc. **176:** 73-202. https://doi.org/10.1111/boj.12197

Trigas, P., Panitsa, M. & Tsiftsis, S. 2013: Elevational gradient of vascular plant species richness and endemism in Crete – the effect of post-isolation mountain uplift on a continental island system. – PLoS ONE **8:** e59425. https://doi.org/10.1371/journal.pone.0059425

—, Tsiftsis, S., Tsiripidis, I. & Iatrou, G. 2012: Distribution patterns and conservation perspectives of the endemic flora of Peloponnese (Greece). – Folia Geobot. **47(4):** 421-439. https://doi.org/10.1007/s12224-012-9130-4

Vander Wall, S. & Longland, W. S. 2004: Diplochory: are two seed dispersers better than one? – Trends Ecol. Evol. **19(3):** 155-161. https://doi.org/10.1016/j.tree.2003.12.004

Vittoz, P. & Engler, R. 2007: Seed dispersal distances: a typology based on dispersal modes and plant traits. – Bot. Helv. **117:** 109-124. https://doi.org/10.1007/s00035-007-0797-8

Vladimirov, V., Aybeke, M., Matevski, V. & Tan, K. (comps.) 2017a: New floristic records in the Balkans: 34. – Phytol. Balcan. **23(3):** 413-444.

—, Aybeke, M. & Tan, K. (comps.) 2017b: New floristic records in the Balkans: 32. – Phytol. Balcan. **23(1):** 119-146.

—, — & — (comps.) 2018a: New floristic records in the Balkans: 35. – Phytol. Balcan. **24(1):** 155-174.

—, — & — (comps.) 2018b: New floristic records in the Balkans: 36. – Phytol. Balcan. **24(2):** 263-292.

—, — & — (comps.) 2019: New floristic records in the Balkans: 40. – Phytol. Balcan. **25(3):** 295-335.

Vuksanović, S., Tomović, G., Niketić, M. & Stevanović, V. 2016: Balkan endemic vascular plants of Montenegro – critical inventory with chorological and life-form analyses. – Willdenowia **46:** 387-397. https://doi.org/10.3372/wi.46.46307

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