Altitudinal patterns of floral morphologies in dry calcareous grasslands

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Abstract

A central goal in vegetation ecology is the identification of processes that influence species assemblage and distribution within a community. Among the wide variety of biotic interactions, plant-pollinator interactions are assumed to have a marked influence on plant communities assemblage and dynamics. The aim of this work was to verify if in dry grasslands there is a non random distribution of different blossom types along an altitudinal gradient, which may exert a selective pressure on both plants and insects, as well as on their mutualistic relationships. We sampled 85 plots in pre-alpine and hilly reliefs of the Veneto Region, finding that different blossom morphologies were patterned along the altitudinal gradient. Wind blossom type was dominant at low altitude while disk shaped flowers prevailed at high altitude. Our study revealed that altitude might affect species assemblage in dry grassland communities not only by selecting plant species according to their tolerance to different environmental conditions, but also according to their floral morphology, evoking the possibility of an indirect pollination filtering to occur.

Key words: blossom types, dry grasslands, habitat filtering, plant species assemblage, pollinators.

Introduction

A central goal in vegetation ecology is the identification of processes that influence species assemblage and distribution within a community. Historically, much consideration has been given to the effects of the environmental conditions in shaping plant communities (Austin, 2007). Indeed, environmental conditions can govern species assemblages by influencing both plants characteristics and adaptations, and the patterns of biotic interactions. Among the wide variety of biotic interactions, authors underlined that pollination is likely to play an important role in structuring natural plant communities (Dante *et al*., 2013; Fantinato *et al*., 2016). Most of flowering plants (angiosperms), by some evaluation up to 86% (Hu *et al*., 2008), show adaptations for pollination by animals, especially insects (39% generalist insects, 27% specialized pollen collecting insects; Hu *et al*., 2008). Given the high diversity of flowering plants and pollinating insects, pollination by animals can be considered a ubiquitous ecological interaction in virtually all terrestrial ecosystems (Memmot *et al*., 2004). Although generalist pollination systems are frequent on a global scale, specialization is also common and it has been assumed to influence angiosperm diversification (Johnson & Steiner, 2000). Most angiosperms produce recognizable suites of convergent floral traits and reward patterns that recur in flowers with different evolutionary origin but that share similar pollinators (Rodríguez-Gironés & Santamaría, 2004; Thomson & Wilson, 2008; Willmer, 2011). According to existing theories (Faegri & Van der Pijl, 1979), pollinators are assumed to select plant species based on distinctive floral traits or blossom types, giving rise to pollination syndromes, namely different combinations of floral characters (e.g. flower shape, accessibility of floral rewards and flower openness). According to the pollination syndrome theory, combinations of floral traits may be used to infer suites of possible pollinators, thereby determining plant species degree of specialization towards pollinators (Fontaine *et al*., 2006; Olesen *et al*., 2007; Westerkamp & Claßen-Bockhoff, 2007). For example, whether blossom types as open disk are accessible to any pollinator, showing a low degree of specialization, bilabiate blossoms are pollinated mainly by bees (order *Hymenoptera*, superfamily *Apoidea*), showing a high degree of specialization (Ramírez, 2003; Westerkamp & Claßen-Bockhoff, 2007). Even if some attention has to be paid when applying these theories to investigate individual plant species reproductive strategies (Giovanetti & Aronne, 2011; Aronne *et al*., 2012), combination of floral traits may be indicative of prevailing trends.

Generally, pollinators are not spread evenly along environmental gradients (Müller, 1881; Kearns, 1992; Bingham & Orthner, 1998; Devoto *et al*., 2005). Some insect groups are sensitive to altitudinal changes, which can affect both their activity and reproductive success (Kearns, 1992; Totland, 1992). Most hymenopterans are widespread in warm and dry conditions, which are typical of low altitudes or latitudes (Müller, 1881; Arroyo *et al*., 1982; Devoto *et al*., 2005; Lázaro *et al*., 2008), while dipterans can forage at very high

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altitudes or latitudes, where they become predominant pollinators (Faegri & van der Pijl, 1979; Arroyo *et al.*, 1982; Kearns, 1992; Totland, 1993; Elberling & Olesen, 1999). Thus, changes in the proportion of different groups of pollinators might lead to changes in the structure and composition of natural plant communities.

European temperate calcareous dry grasslands provide a particularly suitable example to this specific issue. They occur from the lowland to the mountain level, mostly on calcareous to neutral substrates (Calaciura & Spinelli, 2008). Their biological diversity is high and includes a variety of rare species from different taxonomic groups (Van Helsdingen *et al.*, 1996; Ssymank *et al.*, 1998). Among plant communities, dry grasslands rank as one of the richest in species both at small (<1 m2; Purschke *et al.*, 2012; Wilson *et al.*, 2012; Wellstein *et al.*, 2014) and at large habitat spatial scale. High species richness is also found for butterflies and other invertebrates living in these habitats (Bobbink & Willems, 1998; Van Swaay, 2002). Moreover, in Europe, dry grassland habitats are listed in Annex I of the EU Habitat Directive (CE 43/92) as habitats of European interest.

As plant–pollinator interactions play a central role in plant reproduction, they likely have a marked influence on plant community assemblage and dynamics: for example, the absence of a particular group of pollinators can prevent the establishment of a given plant species in specialized pollination systems (Pellissier *et al.*, 2010). Thus a better knowledge of the patterns of blossom types will add new information that may help preserving the habitat and the ecosystem services that it provides (Bartha *et al.*, 2004; Wellstein *et al.*, 2014). Accordingly, the main aim of this work was to verify if blossom types have a structured pattern in the landscape. Especially, we tested if there is a non random distribution of different blossom types along an altitudinal gradient, which may exert a selective pressure on both plants and insects, as well as on their mutualistic relationships.

Study area

The study was conducted in pre-alpine (Cavallo-Visentin Range, Mt. Grappa and Mts. Lessini) and hilly reliefs (Asolani, Marosticani, Berici and Euganei Hills) of the Veneto Region (NE Italy) (Fig. 1; Table 1).

Venetian Pre-Alps, as well as their foothills (i.e. Asolani and Marosticani Hills), originated from an orogenic thrust front resulting from the collision of the Adriatic and the European plates at the end of the Cretaceous (Cuffaro *et al.*, 2010), which caused the lift of marine sedimentary rocks of calcium carbonate. Berici and Euganei Hills lie further south isolated from the Pre-Alps by the northern fringe of the Po plain. Both
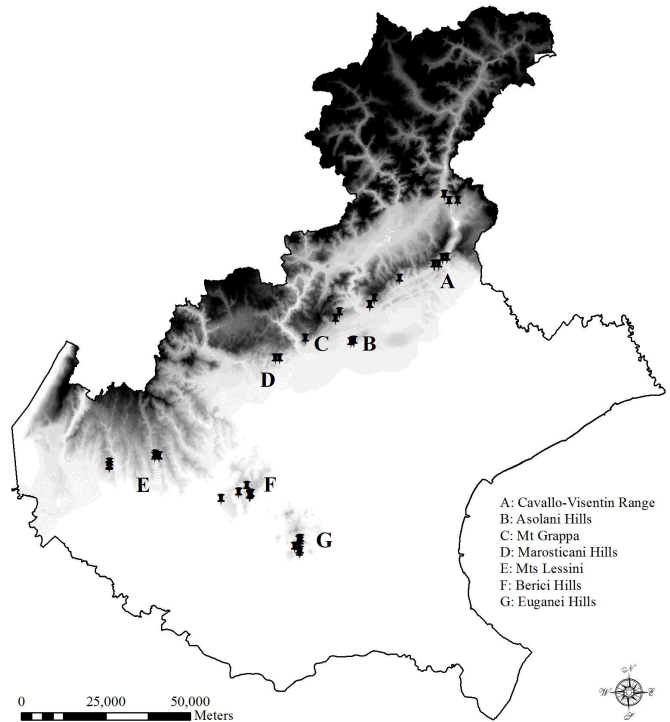

Fig. 1 - Map of the study sites and samples location.

Tab. 1 - Altitude and coordinates (WGS84) of the sampled reliefs.

Relief name	Maximum altitude (m a.s.l.)	Latitude N	Longitude E
Cavallo-Visentin Range	2.472	46.039.224	12.265.774
Mt. Grappa	1.775	45.881.279	11.800.585
Mts. Lessini	1.850	45.546.280	11.044.295
Asolani Hills	496	45.817.382	11.951.327
Marosticani Hills	495	45.772.301	11.653.346
Berici Hills	445	45.443.909	11.516.229
Euganei Hills	601	45.315.955	11.702.056

of them are of volcanic origin (from late Paleocene to late Oligocene; Macera *et al.*, 2003) and are characterized by the co-occurrence of volcanic and calcareous formations. The climate varies from pre-alpine to plain (Barbi, 2012). Cavallo-Visentin range, Mt. Grappa, Mts. Lessini and their foothills (Asolani and Marosticani Hills) show the pre-alpine mesoclimate, with a mean annual temperature of 12°C and mean annual precipitations of 1200 – 1500 mm; while Berici and Euganei Hills show the plain mesoclimate, with a mean annual temperature of 13-14 °C and mean annual precipitations of 800 – 1000 mm (Barbi, 2012).

The study was conducted on semi-natural, oligo-to mesotrophic, *Bromus erectus*-dominated dry grasslands, which establish on poorly developed, shallow and skeletal calcareous soils, characterized by low water retention capacity and high leaching rates (Bini, 2001).

The floristic composition reflects the particular geographic position of the study sites, in a transitional connection area among the Mediterranean, the Alpine and the South-Eastern European phytogeographical regions (Villani *et al*., 2016). The vegetation is normally dominated by few, highly covering, anemophilous species (e.g. *B. erectus*, *Festuca rupicola*, *Artemisia alba*, *Koeleria pyramidata*) and several, scarcely covering, entomophilous species. The most common insect-pollinated species are *Helianthemum nummularium* ssp. *obscurum*, *Teucrium chamaedrys* and *T. montanum*, *Thymus* sp.pl., *Scabiosa triandra*, *Globularia bisnagarica*, *Stachys recta* ssp. *subcrenata*, *Salvia pratensis* ssp. *bertolonii*, *Fumana procumbens* and *Convolvulus cantabrica*. Based on a recent syntaxonomic revision (Terzi, 2015), the investigated dry grasslands can be included in the class *Festuco-Brometea* Br.-Bl. & Tx. ex Klika & Hadač 1944 and the SE-European-Illyrian order *Scorzoneretalia villosae* Kovačević 1959 (=*Scorzonero-Chrysopogonetalia*), represented by several diagnostic species, with high frequency values (*Chrysopogon gryllus*, *Centaurea jacea* ssp. *gaudini*, *Eryngium amethystinum*, *Plantago holosteum*, *S. pratensis* ssp. *bertolonii*, *Sanguisorba minor* ssp. *balearica*, *S. triandra*, etc.). Along the altitudinal range, dry grassland communities can be included in two different alliances. At lower altitude, the community structure is mainly determined by hemicryptophytes and, subordinately, chamaephytes. Given the high percentage of Mediterranean and Illyrian taxa and the phytogeographical and ecological context, the vegetation can be referred to the alliance *Saturejion subspicatae* Tomić-Stanković 1970. At higher altitude, the *Saturejion subspicatae* gives way to the mesoxerophytic alliance *Scorzonerion villosae* Horvatić ex Kovačević 1959. Dry grassland communities of this alliance show a prevalence of hemicryptophytes and of European and Eurasian taxa (Feoli Chiapella & Poldini, 1993; Terzi, 2015) and share many species with the mesophytic meadows of the class *Molinio-Arrhenatheretea* Tüxen 1937 (e.g. *Dactylis glomerata*, *Plantago lanceolata*, *Anthoxanthum odoratum*, *Veronica chamaedrys*).

Materials and Methods

Data collection

Dry calcareous grasslands were sampled in May and June 2014. A total of 85 2x2 m plots (ranging from 82 m a.s.l. to 1453 m a.s.l.) were selected using a stratified random sampling design. During the peak of the community growing season, all vascular plant species were recorded and their percentage cover was visually estimated. Plant nomenclature was standardized following Conti *et al*. (2005; 2007).

For each plot, we recorded altitude and geographical coordinates (UTM – WGS84) by using a commercial GPS (Garmin GPS62s). All the species recorded were classified on the basis of their floral morphology following Pellissier *et al*. (2010). We used six of the seven blossom categories described by Pellisier *et al*. (2010): a) *wind* (e.g. *B. erectus*, *Carex flacca*), usually green inconspicuous flowers, rewardless and nectarfree. They hang anthers and stigmas outside flowers and produce great amounts of light, smooth pollen grains; b) *disk* (e.g. *F. procumbens*, *Geranium sanguineum*), the simplest and most common flower type among existing insect-pollinated species. Disk blossoms usually have a mass of anthers centrally positioned and exposed nectaries. Thus pollen and nectar are generally easily accessible to visitors; c) *funnel* (e.g. *Campanula rapunculus*, *Colchicum autumnale*), open tubular flowers, with central, strongly united stigma and stamens. Nectaries lie at the base of the corolla tube and visitors selection is expected to apply on the basis of body size; d) *bilabiate* (e.g. *S. pratensis*, *Trifolium scabrum* ssp. *scabrum*), zygomorphic tube- or funnel-shaped flowers, characterized by a small and fixed number of concealed stamens, and by totally hidden nectaries. Hence floral resources (pollen and nectar) are accessible only to a narrow group of visitors, which should have a good perception of the flower shape and adequate handling abilities in order to reach resources (Muller, 1995). Food- and sexually-deceptive orchid species (e.g. *Ophrys sphegodes*, *Orchis morio*) were included within this group; e) *tube* (e.g. *Blackstonia perfoliata*, *Silene vulgaris* ssp. *tenoreana*), long tubular corollas, with a fixed number of stamens and totally concealed nectaries. This design usually favours long tongue pollinators (i.e. butterflies and long-tongue bees); f) *head* (e.g. *Centaurea* sp.pl., *S. triandra*), inflorescences of tiny actinomorphic and/ or zygomorphic flowers. These inflorescences usually include two distinctive parts: the outer part, which is made up of ray florets, and the central part, consisting of disk florets. Reproductive organs are generally elongated over the top of corollas, while nectaries are concealed in the bottom. Some head blossoms are constituted by long tubular flowers accessible only to long-tongued insects, whereas others are composed of short flowers that can be easily probed by insects with a short proboscis (i.e. flies and short-tongued bees) (Willmer, 2011).

Data analysis

For each plot we determine the coverage of each blossom type by summing the coverage of plant species belonging to the same blossom category; furthermore, blossom type richness and the evenness (Pielou, 1966) were calculated per plot.

To explore the trend in the distribution of blossom types we performed a Principal Components Analysis

(PCA), based on the relative blossom type coverage matrix.

To highlight possible relationships between blossom types and altitude, Spearman's Rank Correlations were calculated between altitude and the relative coverage of different blossom types, blossom type richness and evenness (Pielou, 1966).

The computations were performed using STATISTICA 8 (StatSoft Inc., 2008; www.statsoft.com).

Results

A total of 254 species of vascular plants were recorded in the 85 sampled plots. The most common species (found in more than half of the plots) were *B. erectus*, *S. minor* ssp. *balearica*, *H. nummularium* ssp. *obscurum*, *T. chamaedrys*, and *Galium verum*. Among the blossom types recorded, disk was prevalent (72 species), followed by bilabiate (70 species), wind (45 species), head (43 species), funnel (15 species) and tube blossoms (9 species). Families were represented by blossom types as follows: 20 families by disk, 11 families by wind, 9 families by bilabiate, 9 families by funnel, 3 families by head, and finally 2 families by tube blossoms. See Table 2 for details about families.

The PCA based on the relative blossom type coverage matrix (Fig. 2) distinguished two groups of plots.

From a floristic point of view, most common species of Group 1 were *B. erectus*, *S. minor* ssp. *balearica*, *T. chamaedrys*, *H. nummularium* ssp. *obscurum*, *S. triandra*, and *G. verum*. The most frequent species present exclusively in Group 1 included *A. alba*, *F. procumbens*, *Dorycnium pentaphyllum* ssp. *herbaceum*, *T. montanum* and *Odontites luteus*. Similarly to Group 1, *B. erectus*, *H. nummularium* ssp. *obscurum*, *G. verum* and *T. chamaedrys* were among the most common species of Group 2. In addition, *Oreoselinum nigrum*, *Stachys officinalis*, *Knautia arvensis*, *F. rupicola*, *P. lanceolata*, *Euphorbia cyparissias*, *Cruciata glabra*, *T. montanum*, *T. pulegioides* and *C. jacea* ssp. *gaudini*, became more common. *K. arvensis*, *Laserpitium latifolium* and *Dianthus monspessulanus*, were the most frequent species present exclusively in Group 2.

The first PCA axis (which explained the 30.67% of the total variance) primarily reflected an altitudinal gradient. In fact, the mean altitude of Group 1 was 332.49 ± 120.1 m a.s.l., while the mean altitude of Group 2 was 997.14 ± 191.59 m a.s.l.. The second axis (17.54% of the total variance) defined a pollination forms gradient, from the prevalence of anemophily at the negative extreme to an increasing presence of entomophily at the positive one. In fact, sampled plots of Group 1 were dominated by highly covering anemophilous species, such as *B. erectus*, *Brachypodium rupestre* and *A. alba*, while sampled plots of Group 2 were more even.

Tab. 2 - Percentage of plant families grouped according to the blossom categories identified in the studied communities.

blossom categories	Family	percentage
Wind	*Poaceae*	62%
	Cyperaceae	13%
	Plantaginaceae	7%
	Others	18%
Disk	*Rosaceae*	17%
	Apiaceae	14%
	Brassicaceae	10%
	Euphorbiaceae	9%
	Rubiaceae	9%
	Caryophyllaceae	6%
	Crassulaceae	4%
	Cistaceae	4%
	Geraniaceae	4%
	Ranunculaceae	4%
	Others	19%
Funnel	*Campanulaceae*	20%
	Rubiaceae	20%
	Asparagaceae	13%
	Convolvulaceae	13%
	Amaryllidaceae	7%
	Apiaceae	7%
	Colchicaceae	7%
	Liliaceae	7%
	Oleaceae	6%
Bilabiate	*Fabaceae*	44%
	Lamiaceae	23%
	Orchidaceae	19%
	Scrophulariaceae	6%
	Others	8%
Tube	*Caryophyllaceae*	86%
	Primulaceae	14%
Head	*Asteraceae*	96%
	Others	4%

Spearman's Rank Correlations (Fig. 3) revealed a decreasing dominance of wind blossoms from low to high altitude, coupled with higher values of blossom type evenness.

Among entomophilous blossom types, disk blossoms showed to prevail significantly at high altitude, while no significant correlations were observed for bilabiate, funnel, head and tube blossoms.

The richness of blossom types didn't change significantly with the altitude.

Discussion

Previous studies (Pellissier *et al.*, 2010) already underlined the importance of altitude in defining floral morphologies distribution in western Swiss Alps as a response to climate variations. Indeed, climate heterogeneity has been proven to affect, inter alia, vegetation distribution and composition (Wang *et al.*, 2006; Gould *et al.*, 2006), life-form spectra (Pavón *et al.*, 2000; Klimeš, 2003, Mahdavi, 2012) as well as pollinator distribution (Müller, 1881; Arroyo *et al.*, 1982; Pellissier *et al.*, 2010). Our results at habitat level confirm the observations made by Pellissier *et al.* (2010).
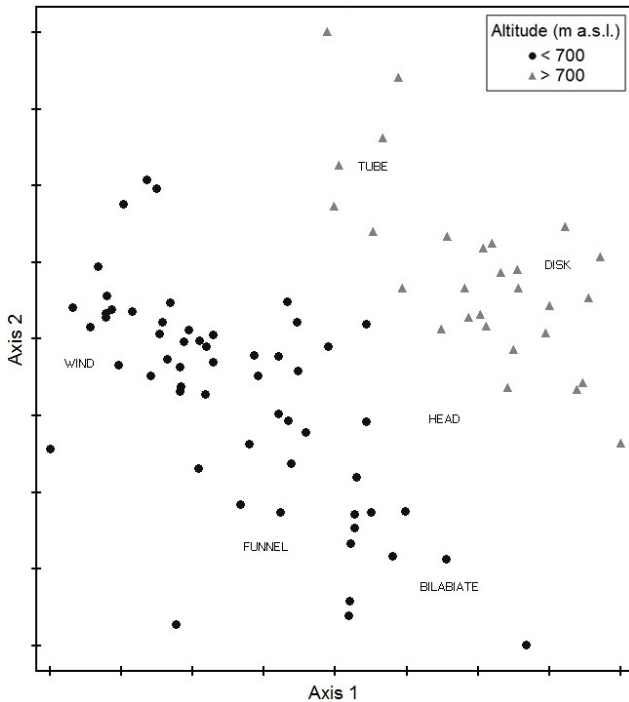
Fig. 2 - PCA ordering of the sampled plots. Sampled plots belonging to different altitudinal groups (threshold level: 700 m a.s.l.) were distinguished with different symbols. Plots belonging to Group 1 (<700 m a.s.l) were shown as black dots, while plots belonging to Group 2 (>700 m a.s.l.) were shown as grey triangles.

Even though the richness of blossom types remained constant when moving from low to higher altitude, two blossom types (wind and disk) changed significantly their relative coverage within dry grassland communities. We found a clear dominance of wind blossoms at low altitude. This result is consistent with the observations made by Pellissier *et al*. (2010), who have hypothesized that precipitation, which increases with increasing altitude, may negatively influence pollen availability and dispersion. Indeed, precipitation in pre-alpine reliefs of the Veneto Region are abundant, making anemophily not be the best pollination option. Our results also match the observations made by Carli *et al*. (2012), who recorded graminoid species (anemophilous) as more abundant in the lowlands, whereas non-graminoid species (mostly entomophilous) were more common in the highlands of Matese dry grasslands. However, in this regard, it is also worth considering the poor knowledge existing on the exploitation of wind blossoms by insects, and their potential contribution to pollination of so-called wind pollinated species (Giovanetti & Aronne, 2011; Aronne *et al*., 2012). If this hypothesis will be verified, wind blossoms distribution may not be driven exclusively by precipitations, but also by pollinators availability.

Disk blossoms were found to be prevalent at high al-

titude, where climatic stressful conditions may limit insect activity. In such a situation, a strategic offer of easily accessible pollen and nectar may guarantee pollination by a wider variety of insects, among which short tongue bees and flies (Pellissier *et al*., 2010). Indeed, despite being considered generally less efficient than hymenopterans, flies are important pollinators of many plants at high altitudes (Arroyo *et al*., 1982; Walker-Larsen & Haarder, 2001). This pattern was observed also by Poldini (1989), who showed an increasing frequency of fly pollinated species in more mature and mesophilous associations, in our case referable to the alliance *Scorzonerion villosae*.

From a broader point of view, the observed blossom patterns may be the result of a combination of processes. Temperate dry grasslands are mostly semi-natural communities maintained by mowing and grazing, which have been proved to regulate species composition and richness (Valkó *et al*., 2011; 2012). Much evidence has been found to indicate that dry grasslands abandoning in the early successional stages results in increasing dominance of grasses such as *B. erectus* or *B. rupestre* and, as a consequence, in decreasing species diversity (Bobbik & Willems, 1987; Bonanomi & Allegrezza, 2004; Biondi *et al*., 2006). Regular mowing in general affects the competitive relationships in grasslands. In particular, restraining dominant graminoids competitors, mowing has been proven to enhance the richness in characteristic grassland forbs. Thus, the abandoning of management practices would lead to an increased dominance of wind blossoms against entomophilous blossom types, which contribute for the most part to the overall diversity in species-rich grassland communities (Wellstein *et al*., 2014; Fantinato *et al*., 2016). Indeed, at higher altitude, dry grassland communities showed an increased evenness of blossom types. This coupled with a greater presence of species of the class *Molinio-Arrhenatheretea* suggests that management activities are still implemented. However, only the most generalist blossom type, i.e. disk, evidenced a significant increase in the relative coverage with altitude, providing further evidence supporting the hypothesis that an indirect pollination filtering exerted by altitude may occur.

Our results highlight the importance of considering the functional relationships between species to gain a deeper knowledge about ecosystem structure and processes. The knowledge of the role played by such interactions could improved management practices or restoration plans, leading to the promotion of the functional conservation of the whole ecological community and ensuring its maintenance over time.

The relationships between pollinators and the reproductive success of flowering plants have been mostly documented at the species level, traditionally focusing on highly specific interactions between one or few
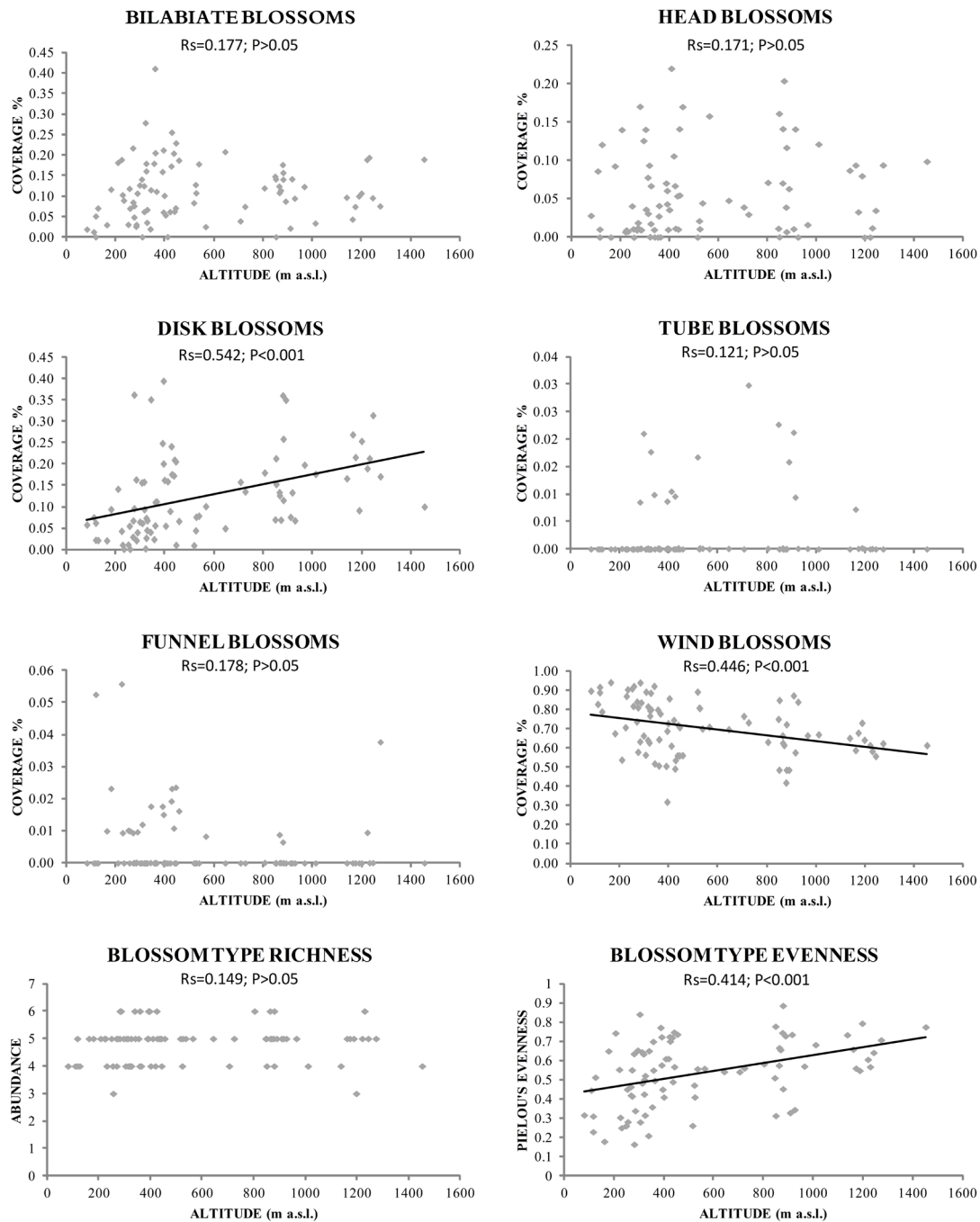
Fig. 3 - Relationships between altitude and blossom type relative coverage, richness and evenness (Spearman's rank correlation coefficients (Rs) and P values). Tendency lines were added to the significant correlations.

plant species and constrained groups of pollinators. Little information is available at the community level, since the study of plant community assembly has rarely considered the role of plant-animal interactions.

However, given the strong dependence of entomophilous species upon pollinators availability for reproduction, we may assume a filter, a selective pressure to the assemblage of plants (Sargent & Ackerly, 2008). Our study suggests that besides the environmental ef-

fect, which selects plant species according to their tolerance to different environmental conditions, altitude might affect the species assemblage in dry grassland communities also through indirect pollination filtering. Studying these interactions may turn out to be essential to disentangle community level processes, e.g. potential competitive or facilitative effects among species, or patterns of community assemblages.

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