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Changes in floristic composition and physiognomy are decoupled along elevation gradients in central Argentina

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Keywords
Chaco vegetation; Conservation; Floristic association; Mountain Chaco; Mountains; Physiognomic types; Restoration; Tree line

Nomenclature
Catálogo de las Plantas Vasculares del Cono Sur (Zuloaga et al. 2008) and online update (www.darwin.edu.ar), except *Schinopsis marginata* (Muñoz 2000) and *Vachellia* (www.tropicos.org)

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Abstract

Questions: Most vegetation descriptions tacitly assume that floristic composition and physiognomy are tightly linked. However, the two vegetation properties may not respond in a similar way to environmental and disturbance gradients, leading to uninformed management planning and difficulties when attempting to restore degraded ecosystems. In this context, we addressed two main questions: (1) how close are relations between floristic and physiognomic types as defined by numerical vegetation classification in mountain ecosystems; and (2) how are floristic and physiognomic types distributed along the elevation gradient?

Location: Central mountains of Argentina, between 500 and 1700 m a.s.l.

Methods: We selected 437 sites where we performed complete floristic and physiognomic relevés. We classified eight physiognomic and eight floristic types. We tested the relationship between the two classifications through a chi square analysis. We tested the association between elevation and each physiognomic and floristic type with random permutations.

Results: In general, floristic types were significantly and positively associated with more than one physiognomic type and *vice versa*. Physiognomic and floristic types responded differently to the elevation gradient. Floristic types were restricted to different sections of the gradient, although having large overlap among them. In contrast, seven out of the eight physiognomic types did not show elevation restriction, being distributed along the complete elevation gradient. The open low woodland with shrubs was the only restricted physiognomy, significantly absent from the upper part of the gradient.

Conclusions: We highlight the importance of considering the two vegetation properties independently when characterizing vegetation patterns in heterogeneous systems, since they show decoupled responses to environmental gradients. We note that the assumption of a direct link between floristic composition and physiognomy may induce bias into the understanding of vegetation patterns and processes. Hence, we encourage managers and restoration practitioners to consider the complete range of possible physiognomic types under each floristic type.

Introduction

Floristic composition and physiognomy are relevant vegetation properties, commonly used to describe vegetation patterns and shifts in plant distribution along environmental gradients (Whittaker 1967; Jennings et al. 2009). The former property is related to the taxonomic identity of plants, while the latter refers to the horizontal and vertical biomass distribution (Shimwell 1971; Jennings et al. 2009). To some extent, plant species composition and physiognomy are linked, as plant growth form and architecture are evolutionarily

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constrained within each species. However, some characteristics inherent to plant growth form (e.g. size and height), as well as the abundance of one particular species may vary according to local disturbance-associated biotic and abiotic factors, such as herbivory or fire (e.g. Whittaker 1962; Grau & Veblen 2000; Pyke et al. 2001; Cairns & Moen 2004; Paruelo et al. 2004; Giorgis et al. 2010). As a result, sites with similar floristic composition may show a notably different physiognomy (Westhoff 1967; Pignatti et al. 1995; Carrión & Fernández 2009; Carrión 2010). For example, a number of authors reported prominent shifts in physiognomy (e.g. from forests to shrublands, or from tall to short grasslands) along grazing or other disturbance gradients, without discernible changes in floristic composition (Felfili et al. 2000; Cingolani et al. 2003; Paruelo et al. 2004; Conti & Díaz 2013). On the other hand, abiotic environmental factors such as climate or topography usually affect floristic composition, but not necessarily physiognomy. Hence, it is common to observe shifts in floristic composition under the same physiognomic type along environmental gradients (Whittaker 1956). For example, some authors have reported shifts in forest types along elevation gradients (Cabido et al. 1991; Li et al. 2013). These observations indicate that the relationship between floristic composition and physiognomy is not a tight one, and that the two properties may respond differently to different factors.

Despite the above-mentioned observations, traditional vegetation descriptions often assume that sites characterized by a particular floristic composition share the same physiognomy (Whittaker 1962; Jennings et al. 2009). This implicit assumption is evident when naming floristic types as a result of vegetation classifications. Floristic types are usually named after the dominant species (Shimwell 1971; Carrión 2010), followed by terms describing their physiognomy (e.g. *Pseudotsuga menziesii* forest, Jennings et al. 2009; *Artemisia cana/Leymus cinereus* shrubland, Cooper et al. 1999). Although some authors have recognized difficulties when attempting to assign a unique physiognomy to a given floristic type (e.g. Pignatti et al. 1995), the tradition persists until now (e.g. Faber-Langendoen et al. 2014). Hence, only one out of various possible physiognomies are recognized for each floristic type, which is generally the dominant physiognomy (i.e. the most widespread in the landscape), but not necessarily the potential one (i.e. that which would dominate in absence of disturbance).

The implicit link between floristic composition and physiognomy in vegetation classifications may lead to two different problems when attempting to use these classifications for conservation or restoration purposes. First, it may be assumed that both properties respond in the same way to biotic and abiotic factors, producing uninformed selection of reference systems for restoration purposes. For example, a floristic type may be selected as reference system, linked with a given physiognomy that could be the most frequent, but not necessarily the potential physiognomy in a given habitat. In such cases, when eliminating disturbance to attain the conservation or restoration of the area, unexpected changes may occur (e.g. woody encroachment) (Asner et al. 2004; Maestre et al. 2016). Second, it may lead to the use of only physiognomic, or only floristic properties when selecting indicators for restoration or conservation monitoring. The selection of representative and useful indicators is a key and controversial point in ecosystem management (Clewell & Aronson 2007). While some authors argue that indicators related to physiognomy are adequate (Durigan & Suganuma 2015; Suganuma & Durigan 2015), others suggest that the use of floristic indicators is essential (e.g. Leighton Reid 2015). In summary, the failure to recognize that floristic composition and physiognomy are not always tightly linked and do not necessarily respond in a similar way to the same biotic and abiotic factors, may lead to uninformed management planning and difficulties when attempting to restore degraded ecosystems and select indicators (Pignatti et al. 1995; Carrión 2010).

The effective conservation, management and restoration of species, communities and ecosystems in mountain environments demand a deep understanding of vegetation responses along environmental gradients (Lamb & Gilmour 2003; Temperton & Hobbs 2004; Clewell & Aronson 2007). We suggest that the floristic perspective and the physiognomic perspective may be integrated in a single approach but treated as independent vegetation properties. In this contribution we illustrate this approach using as an example from the mountains of central Argentina.

In mountain ecosystems, vegetation patterns are mainly framed by elevation, which produces a climatic gradient of decreasing temperature from base to top, often accompanied with precipitation variations (Körner 1999). Secondarily, the elevation gradient may be associated with the disturbance regime (Nogués-Bravo et al. 2008). In different regions worldwide, traditional vegetation descriptions have divided this gradient into altitudinal belts characterized by one floristic composition directly linked to a single physiognomic type (e.g. Hemp 2006). Following this tradition, the vegetation of the central mountains in Argentina has been historically divided into different altitudinal belts, ranging from xerophytic woodlands in the lower slopes, followed by shrublands at intermediate elevations and grasslands mixed with high mountain woodlands in the upper parts (Luti et al. 1979; see study area section for more details). For the lower altitudinal belts, detailed floristic descriptions were performed by Cabido et al.

(1991), describing shifts in the floristic composition of xerophytic woodlands between 450 and 1050 m a.s.l., and by Cantero et al. (2001) describing shifts in grassland floristic composition between 900 and 1800 m a.s.l. However, each of those studies addressed only one physiognomic type (woodlands or grasslands, respectively), assuming that xerophytic woodlands are climatically restricted to the lower elevations, and neither of them described possible physiognomic variation among and within floristic types. This assumption was later challenged through the evaluation of a transitional zone between 900 and 1100 m a.s.l., which suggested that the upper limit of the xerophytic woodland is not primarily conditioned by temperature, but rather determined by fire and domestic grazing (Giorgis et al. 2013). Similar findings were reported in other transitional zones between forests and grasslands in mountain ecosystems around the world (Cairns & Moen 2004; Behling & Pillar 2007; Gehrig-Fasel et al. 2007; Coop et al. 2010).

In this context, the objectives of this study were to: (1) classify and characterize independently the floristic composition and physiognomy of the xerophytic woodland and shrubland belts (500–1700 m a.s.l., *sensu* Luti et al. 1979) in Cordoba mountains; (2) evaluate the relationship between the floristic and physiognomic classifications; and (3) compare the distribution patterns of floristic and physiognomic types along the elevation gradient.

Methods

Study area

The study was carried out in the mountains of Córdoba in central Argentina. These mountains are formed by three main ranges that run 430 km from north to south (29°00′ S–33°12′ S) and 110 km from east to west (64°18′ W–65°29′ W). Their elevation varies from *ca*. 500–2790 m a.s.l., with Mt. Champaqui being the highest peak (Fig. 1).

As in a typical mountain system, the climate in our study area is framed by the elevation gradient. At 500 m a.s.l., in the centre of the latitudinal range, mean annual temperature is 17 °C, while at 1800 m a.s.l. it is 11.2 °C, and at 2700 m a.s.l. 7.4 °C (De Fina 1992; Marcora et al. 2008). Along with the cooling of climate as elevation increase, precipitation and soil moisture content also increases (Colladon 2014; Tecco et al. 2016). At the upper parts of the mountains, mean annual precipitation reaches 900 mm, while at low elevations there is a marked rainfall regional gradient from east (annual rainfall >700 mm) to west (annual rainfall <500 mm), with most rainfall concentrated in the warmer months. Additionally, temperature tends to decrease slightly from north to south (Capitanelli 1979; Giorgis et al. 2015).

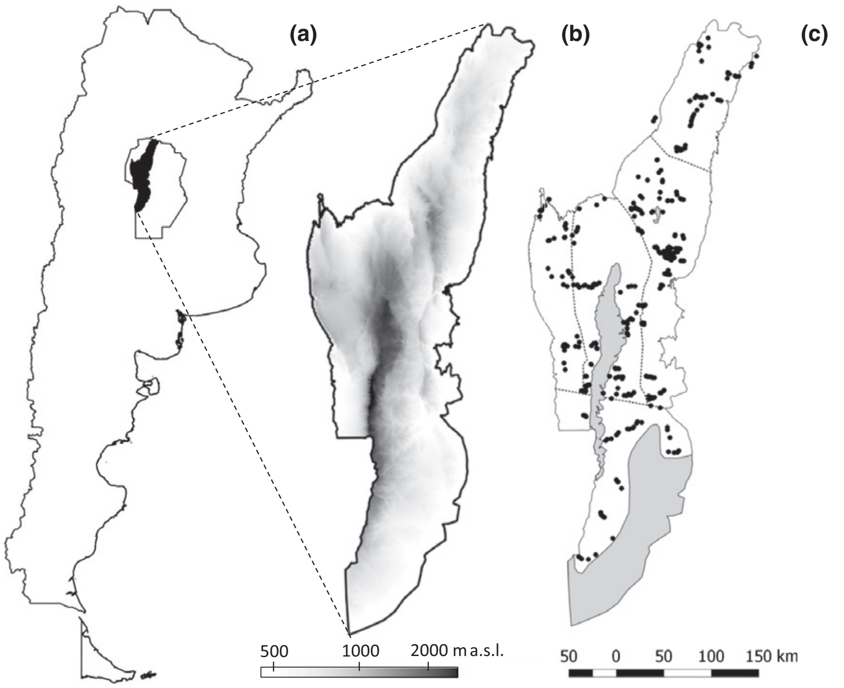

Fig 1. (**a**) Location of the study area (■) in Córdoba Province in Argentina. (**b**) Elevation gradient in the study area. (**c**) Distribution of the 437 relevés in the five sectors of the study area (⬚). Agricultural zones in the lower plains and the sub-Andean zone above 1700 m were not sampled (▨).

Current vegetation description of the study area

According to traditional descriptions, the vegetation of the central mountains in Argentina belongs to the Chaco Serrano district, within the Chaco phytogeographic province (Cabrera 1976). The Chaco Serrano vegetation dominates the slopes of the mountains of central and northwest Argentina, and southern Bolivia, and forms complex ecotones with upper mountain ecosystems, as well as with woody communities dominating the Chaco-Pampean plains (Prado 1993). The floristic knowledge of the Chaco Serrano, as well as the relationships with other neighbouring ecosystems is scarce throughout its whole extension.

Considering the identity of the dominant plant species, the vegetation of the central mountains of Argentina has been historically divided into different altitudinal belts. Kurtz (1904) described two main belts: the low-mountain woodland zone in the lower part and the sub-Andean zone above 1700 m a.s.l. In turn, Luti et al. (1979) divided the Chaco Serrano district into three altitudinal belts. According to this description, the mountain xerophytic woodland belt, dominated by *Schinopsis marginata* and *Lithraea molleoides*, occupies the lower part of the gradient (between 500 and 1300 m a.s.l.), followed by the mountain shrubland belt (locally named Romerillal) dominated by *Baccharis aliena* (up to 1700 m a.s.l.). Finally, the grassland belt with patches of high-mountain *Polylepis australis* woodlands occupies the upper part of the mountains (up to 2790 m a.s.l.).

Selection of study sites

To achieve a representative sampling, we divided the mountains into three areas: one area in the north, one area in the south and one in the centre, which in turn was divided into an east-central, middle-central and a western-central area (Fig. 1). Additionally, to focus our attention on the Chaco vegetation, we excluded the upper part of the mountains since the vegetation belt above 1700 m has been related to the Andean and Patagonian flora and vegetation (Cabido et al. 1998; Martínez et al. 2017). As the lower limit we considered the elevation of 500 m a.s.l. proposed by both Kurtz (1904) and Luti et al. (1979) as the transition zone between lowland ecosystems and the mountain ecosystems corresponding to the Chaco Serrano district (Cabrera 1976). However, due to some variation in the limits along the latitudinal gradient some sites were located slightly above and below to that elevation.

During field trips in the growing seasons (Dec to Mar) of 2006 to 2009 we selected and sampled a total of 437 homogeneous sites of 20 m × 20 m. We used a preferential stratified sampling design. Sites were stratified between the five areas and represented all vegetation patch types within them (Fig. 1). We included some sites in pine plantations because they have an important cover in these mountains (13,000 ha). Moreover, *Pinus* species are escaping from plantations (Giorgis et al. 2011a) and could potentially cover the complete elevation gradient (Urcelay et al. 2017), as is happening in others ecosystems in South America (Zalba et al. 2008; Orellana & Raffaele 2010; Simberloff et al. 2010).

Data collection

At each of the 437 sites we recorded latitude, longitude and elevation with a GPS and performed a complete floristic relevé comprising all vascular plant species present. We visually estimated the cover (%) of each species (from + for species with <1%, then 1, 2, 3, 5, 8, 10%, and thereafter with increment ranges of 5% until 100%). As physiognomic properties we estimated the maximum height of vegetation (cm), mean height (cm) and cover (%) of the herbaceous, shrub and tree layers, and total vegetation cover. These properties provide a three-dimensional representation of the biomass vegetation distribution (Jennings et al. 2009). The tree layer was defined by the presence of woody plants >4-m tall, while the shrub layer was defined by the presence of woody plants <4-m tall (modified from Jennings et al. 2009). The herbaceous layer was defined by the presence of herbaceous vascular species rooted on the ground. Epiphytic herbaceous plants were recorded in some sites, but in general they had very low cover. It is important to note that the addition of the three layers' cover may exceed 100%, because layers may overlap.

Data analyses

We used TWINSPAN to classify relevés into different groups of floristic composition (MjM Software Design, Gleneden Beach, OR, US). We used a matrix of 437 relevés × 776 species, as species with a single presence were removed from a total of 893 species (Microcomputer Power, Ithaca, NY, US; Kent 2011). For this analysis we transformed cover data into the following scale: 1 (cover <1%, annotated with + in the field), 2 (cover from 1% to 5%), 3 (cover from 6% to 15%), 4 (cover from 16% to 35%), 5 (cover from 36% to 70%) and 6 (cover from 71% to 100%; adapted from Jennings et al. 2009). We considered the eight groups of relevés segregated at the third division level. Each floristic type was named after the genus of the species with highest average cover present in >40% of the relevés (i.e. constancy of III or more; see Appendix S2 for more details on the constancy index), followed by the genus of the second most abundant species present in >80% of the relevés (i.e. constancy V).

For physiognomy we performed a K-means classification procedure (Jain & Dubes 1988). We used a matrix of 437 relevés × six physiognomic variables: total vegetation cover (%), cover of the tree, shrub and herbaceous layers (%), maximum height of the vegetation within the site (cm) and, finally, the mean vegetation height in the site (cm). This last variable was estimated as the average height of the different layers weighted by their cover (more details in Appendix S1). We standardized the values of the maximum and the mean vegetation height to vary in a similar range as the other variables (from 0 to 100). Eight clusters were identified as physiognomic types, and each of them was named considering the tallest and the dominant layers. In some cases we used the term 'open' or 'closed' to differentiate between some types of shrublands or woodlands according to the cover of the shrub or tree layer, respectively.

We chose TWINSPAN for floristic data, because it has proven adequate in several comparisons of classification techniques, especially for long floristic gradients with many zero entries in the data matrix (Cao et al. 1997; Moss et al. 1999; Wesche & von Wehrden 2011). For physiognomic classification, we selected K-means clustering because it is stable and performs well for variables with few zero entries in the data matrix (Jain 2009).

We analysed the relationship between the eight floristic and the eight physiognomic types through a contingency table. Based on this table, we performed a chi-square test and goodness-of-fit tests (Agresti 2007) using the R package 'stats' (R Foundation for Statistical Computing, Vienna, AT). In this way, we detected positive and negative significant associations between the groups obtained with the two classifications.

We estimated the mean elevation and the elevation amplitude of each physiognomic and floristic type to describe their elevation range of occurrence. The mean elevation was calculated by averaging the elevation of all relevés included in each group (floristic or physiognomic), and the amplitude was calculated as the difference between the maximum and the minimum elevation within each group. We tested if the mean elevation and the elevation amplitude of each physiognomic and floristic type were significantly different than expected by chance. For this we performed 1000 random permutations of the elevation position of the relevés. We considered that the mean elevation was significantly different from chance expectation when its value was higher or lower than the 95% of the expected average values. For elevation amplitude, we considered that it was significantly shorter than chance expectation when its value was lower than 95% of the expected average values.

Results

Floristic and physiognomic classifications

The TWINSPAN based on floristic composition first divided all relevés into two major groups (Fig. 2). In the two subsequent divisions, the first group was divided into four floristic types characterized by a higher abundance of *Festuca hieronymi* grasses or *Vachellia caven* (ex *Acacia caven*) shrubs or small trees, while the second group was divided into four floristic types characterized by a higher abundance of the tree species *L. molleoides*, *Ligustrum lucidum* and/or *S. marginata*. Noteworthy, *L. lucidum* is not native (i.e. Asiatic) unlike the rest of the species that characterize the floristic types (see more details of floristic types in Table 1 and Appendices S2 and S3). The least represented floristic type was *Festuca-Piptochaetium* (A), with only 7% out of the 437 sites, while the most represented were the two types dominated by *V. caven* (C and D), which accounted for the 41% of the sites, being the most extended floristic types along the elevation gradient (Table 1, Fig. 2, Appendix S3).

The eight physiognomic types varied from an average height of 72 cm for the herbaceous type, up to a maximum of 13 m for the tallest woodland type (Table 2, more details in Appendix S4). The least represented physiognomic type was the open low woodland with shrubs (5), with only 4% out of the 437 sites, while the most prevalent was the herbaceous type (1) with 22% of the sites.

Floristic vs physiognomic types

Out of the 64 cells resulting from the combination of the eight physiognomic and the eight floristic types, only 19 (29.7%) were empty (Table 3). This indicates that each floristic type can adopt various physiognomies, and each physiognomic type can include various floristic types. However, the relationship between floristic and physiognomic types was different than expected by chance ($\chi^2 = 508.33$, $P < 0.0001$), indicating positive and negative significant associations among them.

The floristic types most tightly linked to physiognomy *Festuca-Piptochaetium* (A), *Festuca-Cantinoa* (B) and *Schinopsis-Vachellia* (G), each of them harbouring various physiognomic types, but with only one type significantly and positively associated (Table 3). With the opposite behaviour, the *Lithraea-Celtis* (E) and *Ligustrum-Lithraea* (F) types, harboured all or most of the eight physiognomic types, with two or three of them (different types of woodlands) significantly and positively associated (Table 3).

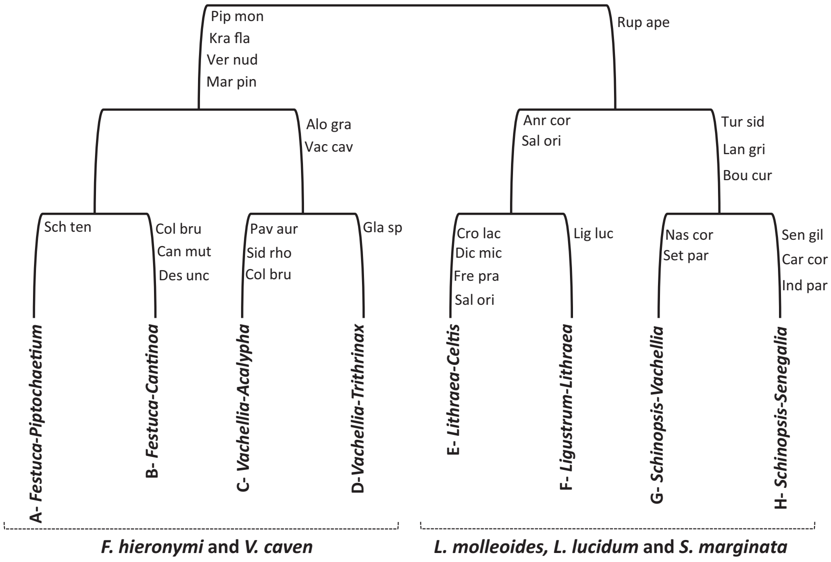

Fig. 2. Successive divisions of TWINSPAN based on floristic composition. For each division, indicator species are shown: *P. montevidense* (Pip mon), *Krapovickasia flavescens* (Kra fla), *Vernonanthura nudiflora* (Ver nud), *Margyricarpus pinnatus* (Mar gin), *Ruprechtia apetala* (Rup ape), *Aloysia gratissima* (Alo gra), *V. caven* (Vac cav), *Anredera cordifolia* (Anr cor), *Salpichroa origanifolia* (Sal ori), *Turnera sidoides* (Tur sid), *Lantana grisebachii* (Lan gri), *Bouteloua curtipendula* (Bou cur), *Schizachyrium tenerum* (Sch ten), *Cologania broussonetii* (Col bru), *C. mutabilis* (Can mut), *Desmodium uncinatum* (Des unc). *Pavonia aurigloba* (Pav aur), *Sida rhombifolia* (Sid rho), *Glandularia* sp. (Gla sp), *Croton lachnostachyus* (Cro lac), *Dichondra microcalyx* (Dic mic), *Fleischmannia prasiifolia* (Fre pra), *L. lucidum* (Lig luc), *Nassella cordobensis* (Nas cor), *Setaria parviflora* (Set par), *S. gilliesii* (Sen gil), *Cardiospermun corindum* (Car cor), *Indigofera parodiana* (Ind par). At the lower end of the tree, the eight floristic types (A–H) are named by their two most representative species (i.e. most abundant and constant; see Methods for more details). Finally, the dominant species of the two main groups (after the first division) are highlighted at the bottom of the diagram.

Table 1. Average ± SE of richness, evenness and diversity (Shannon index) for each floristic type.

Floristic Types	Richness	Evenness	Diversity
A - *Festuca-Piptochaetium*	81.6 ± 3.6	0.98 ± 0.01	4.3 ± 0.05
B - *Festuca-Cantinoa*	74.5 ± 3.4	0.98 ± 0.01	4.2 ± 0.06
C - *Vachellia-Acalypha*	81.5 ± 1.7	0.98 ± 0.00	4.3 ± 0.02
D - *Vachellia-Trithrinax*	80.0 ± 1.5	0.98 ± 0.00	4.3 ± 0.02
E - *Lithraea-Celtis*	57.5 ± 1.5	0.97 ± 0.01	3.9 ± 0.03
F - *Ligustrum-Lithraea*	40.5 ± 2.3	0.96 ± 0.00	3.5 ± 0.08
G - *Schinopsis-Vachellia*	62.4 ± 2.2	0.97 ± 0.01	4 ± 0.04
H - *Schinopsis-Senegalia*	61.3 ± 1.6	0.98 ± 0.01	4 ± 0.04

The physiognomic types most tightly linked with floristic types were two types of woodland (5 and 7), with the strongest link between open woodland with shrubs (5) and *Schinopsis-Senegalia* (H). The remaining physiognomic types harboured more than four or five floristic types, each of them with two significantly and positively associated floristic types (Table 3).

The elevation gradient

All the floristic types showed narrower elevation amplitudes than expected by chance, indicating that all of them tend to be restricted to a given section of the elevation gradient (Fig. 3a). Accordingly, most of them also showed a different mean elevation than expected by chance, except the two types distributed at intermediate elevations. The distribution of *Schinopsis-Senegalia* (H) was significantly restricted to the lower elevation extreme of the mountains.

Table 2. Mean values of diagnostic variables for each physiognomic type. (1) Herbaceous type (2) degraded herbaceous type with shrubs; (3) open shrubland; (4) closed shrubland; (5) open low woodland with shrubs; (6) open low woodland with herbs; (7) closed low woodland; (8) closed tall woodland.

Variable	1	2	3	4	5	6	7	8
Total Vegetation Cover (%)	94.7	66.1	91.0	81.3	93.4	95.8	98.0	92.7
Tree Cover (%)	3.0	1.7	5.3	6.5	49.2	66.0	89.0	80.2
Shrub Cover (%)	13.8	21.3	50.3	62.0	64.7	23.0	30.3	15.5
Herb Cover (%)	90.1	50.9	72.7	30.7	38.1	79.0	26.7	18.7
Max Height (cm)*	328.5	264.2	418.5	572.4	911.1	840.0	801.9	1264.3
Mean Height (cm)*	71.9	74.1	115.8	160.3	349.8	303.2	443.5	741.6

*Non-standardized values.

Table 3. Relationship between physiognomic and floristic types. Each cell shows the difference between the observed frequency and the frequency expected by chance (OBSERVED – EXPECTED) and provide the actual observed frequency between brackets. The final column and row show the total number of sites in each physiognomic and floristic type, respectively. Significant values are highlighted in bold and with an asterisk.

			Floristic types								
			A *Festuca-Piptochaetium*	B *Festuca-Cantinoa*	C *Vachellia-Acalypha*	D *Vachellia-Trithrinax*	E *Lithraea-Celtis*	F *Ligustrum-Lithraea*	G *Schinopsis-Vachellia*	H *Schinopsis-Senegalia*	Total number of sites
Physiognomic types	1	Herbaceous type	3.6 (10)	**15*** (24)	**13*** (34)	5.3 (23)	−**15*** (1)	−**6*** (0)	−**8*** (2)	−**9*** (0)	94
	2	Degraded herbaceous type with shrubs	**14** (18)	−2 (3)	−4 (8)	4.6 (15)	−**9*** (1)	−4 (0)	−**5*** (1)	*4 (9)	55
	3	Open shrubland	−**6*** (0)	−**5*** (2)	**16*** (34)	**13*** (28)	−5 (9)	−4 (2)	−2 (6)	−**7*** (0)	81
	4	Closed shrubland	−**5*** (0)	−**6*** (1)	−**10*** (7)	2.3 (17)	−**8*** (5)	−**5*** (0)	**17*** (25)	**16*** (23)	78
	5	Open low woodland with shrubs	−1 (0)	−2 (0)	−**4*** (0)	−3 (0)	*2.9 (6)	0.8 (2)	2.2 (4)	**4.4*** (6)	18
	6	Open low woodland with herbs	−2 (0)	−1 (2)	1.8 (9)	−**6*** (0)	**5.3*** (11)	**3.8*** (6)	−1 (2)	−3 (0)	30
	7	Closed low woodland	−4 (0)	−**5*** (0)	−**11*** (1)	−**10*** (0)	**26*** (35)	**9.4*** (13)	−1 (4)	−**5*** (0)	53
	8	Closed tall woodland	0.1 (2)	2.4 (5)	−3.1 (3)	−**5.3*** (0)	3.2 (8)	**5.1*** (7)	−1.9 (1)	−0.5 (2)	28
Total number of sites			30	37	96	83	76	30	45	40	437

χ^2 test = 508.33, *P* = ≤0.0001.

It showed both the lowest mean and shortest amplitude among all floristic types. Indeed, the other two floristic types characterized by tree species, *Lithraea-Celtis* (E) and *Schinopsis-Vachellia* (G), were also restricted to the lower part of the elevation gradient (Fig. 3a), but in both cases the restriction was less severe than for the previous type (H). The *Vachellia-Acalypha* type (C) was restricted to the lower and central parts of the gradient, although its mean elevation (1000 m a.s.l.) was slightly but significantly higher than expected by chance (Fig. 3a). The floristic types *Ligustrum-Lithraea* (F) and *Vachellia-Trithrinax* (D) were restricted to the intermediate part of the elevation gradient. Finally, the two floristic types dominated by a tall tussock grass (A: *Festuca-Piptochaetium* and B: *Festuca-Cantinoa*) were restricted to the upper part of the gradient (Fig. 3a), with their mean elevations higher than expected by chance.

In contrast to floristic types, seven out of the eight physiognomic types did not show elevation restrictions, as their elevation amplitude was not different than expected by chance (Fig. 3b). Open shrubland (3), open low woodland with herbs (6), closed low woodland (7) and closed tall woodland (8) occur indistinctly at any elevation. Both herbaceous types (1 and 2) were present at any elevation, but tend to occur preferentially at the upper part of the gradient, as evidenced by their means higher than expected by chance, while closed shrubland (4) is also present at any elevation but occurs preferentially at low elevations (Fig. 3b). Finally, open low woodland with shrubs (5) showed a significant restriction to the low and medium parts of the gradient (Fig. 3b).

Discussion

Decoupled relationship between floristic composition and physiognomy

Our results indicate that a given floristic type may include various physiognomic types. In line with warnings from previous authors (Westhoff 1967; Pignatti et al. 1995; Carrión & Fernández 2009; Carrión 2010), this finding highlights the mistake of linking one floristic type with a single physiognomy. While the results of this approach may vary slightly depending on the classification techniques used, whose selection is somewhat subjective, the main conclusions do not change. We tested different options, and with all of them we found a decoupled relationship between floristic and physiognomic classifications (results not shown).

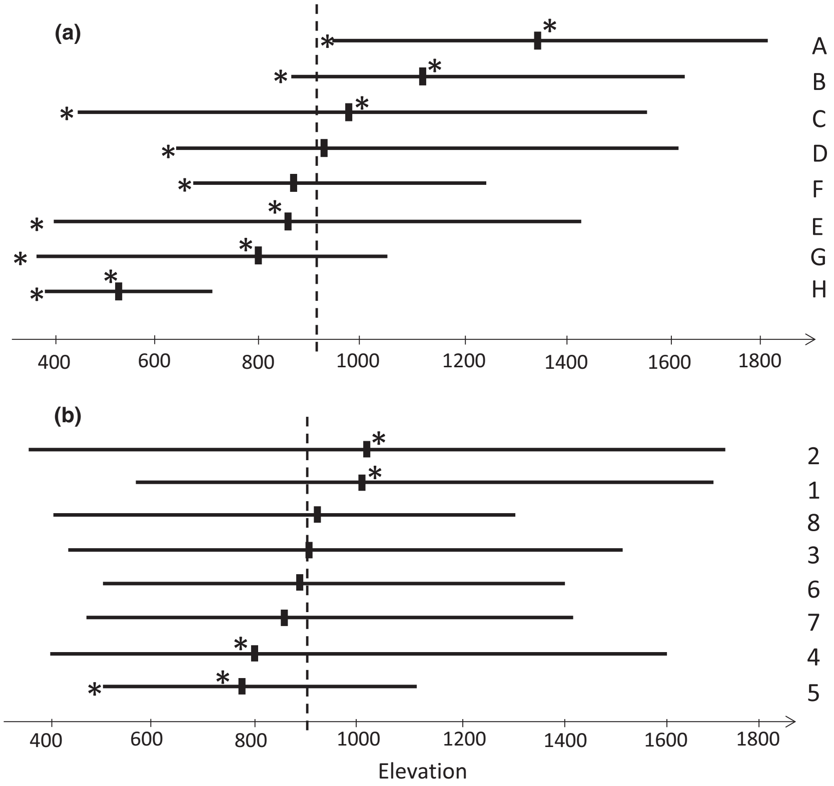

Fig. 3. Amplitude and mean elevation, indicated by horizontal and short vertical lines, respectively, along the elevation gradient for each floristic type (**a**) and for each physiognomic type (**b**). Both types are ordered according their mean altitude. Significant differences from chance expectations are indicated with an asterisk (*). When the asterisk is plotted at the right of the mean it indicates significantly higher altitude than expected by chance, while the asterisk at the left of the mean indicates significantly lower altitude than expected by chance. An asterisk at the left of the horizontal line indicates significantly shorter elevation amplitude than expected by chance. The vertical dotted line indicates the average altitude expected by chance (i.e. mean elevation value of the 437 sites = 915.8 m a.s.l.). Floristic types; (A) *Festuca-Piptochaetium*, (B) *Festuca-Cantinoa*, (C) *Vachellia-Acalypha*, (D) *Vachellia-Trithrinax*, (E) *Lithraea-Celtis*, (F) *Ligustrum-Lithraea*, (G) *Schinopsis-Vachellia*, (H) *Schinopsis-Senegalia*. Physiognomic types; (1) herbaceous type; (2) degraded herbaceous type with shrubs; (3) open shrubland; (4) closed shrubland; (5) open low woodland with shrubs; (6) open low woodland with herbs; (7) closed low woodland; (8) closed tall woodland.

The decoupled relationship between floristic and physiognomic types was particularly striking in the case of *Vachellia* types (C and D) dominated by a woody species but showing a large proportion of sites adopting a herbaceous physiognomy. This is driven by the occurrence of numerous subordinate herbaceous species, which reach as a group far higher cover than the dominant species *V. caven*. Similarly, a tall woodland physiognomy (8) was rather the exception than the rule among floristic types dominated by native tree species (i.e. 10.5%, 2.2% and 5% of the cases for floristic types E, G and H, respectively), which in most cases adopt the physiognomy of closed shrublands or low woodlands (4–7). Since trees of *L. molleoides* and *S. marginata* may reach heights of 15–20 m, our results clearly show that the current floristic types dominated by native trees are far away from their potential expression described with traditional approaches (Cabrera 1976; Luti et al. 1979).

The overall contrasting biomass distribution observed within each native floristic type might be explained by the overwhelming resprouting capacity of our woody species (e.g. *L. molleoides, V. caven, R. apetala, P. australis*) in response to fire (Renison et al. 2002; Gurvich et al. 2005; Torres et al. 2014) and grazing (Giorgis et al. 2010). Fire on a woodland physiognomy produces a drastic reduction in woody biomass followed by an increase in herbaceous vegetation. However, woody species resprout from the base, and a few years after the fire event, floristic composition became quite similar to the previous one, while physiognomy needs more time to recover. The recovery of physiognomy is particularly slow if the area is under high grazing pressure by domestic herbivores, because animals browse the new shoots, slowing down the growth of trees and shrubs (Giorgis et al. 2010; Torres & Renison 2015). In this way, a high cover of herbaceous plants is maintained, which may produce a positive feedback with fire, preventing succession towards the full recovery of woody physiognomies (Giorgis et al. 2013; Argañaraz et al. 2015). In summary, disturbance is a major driver of physiognomic changes in our system as well as in other systems (Dantas et al. 2016), but seems to be a less important driver of floristic composition variations (Paruelo 2005).

Our approach may be used as a framework to hypothesize about successional relationships within and between floristic types occupying similar elevation ranges. For example, the floristic type of *Lithraea-Celtis* (E) adopts four main physiognomies (the four types of woodlands), which may be interpreted as different stages of post-disturbance succession. Further successional relationships could be inferred between this floristic type, which has high constancy of *V. caven,* and the *Vachellia-Acalypha* type (C), which has relatively high constancy of *L. molleoides* and *C. ehrenbergiana*. This last floristic type (C), mostly found as herbaceous and shrubland physiognomic types, could then be expected to change into woodlands of *Lithraea-Celtis* type (E) in the absence of disturbance, as was suggested by Giorgis et al. (2013). Similarly, in the case of the floristic type of *Schinopsis-Vachellia* (G), the conversion from shrubland into woodland in the absence of disturbance could be proposed. Additionally, the floristic type (F) co-dominated by an alien tree (*L. lucidum*) is closely related to *Lithraea-Celtis* type (E). As woody invasion in the system is currently conditioned by propagule pressure (Giorgis et al. 2011a, 2016), our results suggest an alternative successional pathway when availability of *L. lucidum* propagules increases (e.g. Zeballos et al. 2014). These examples illustrate the type of hypotheses that can be proposed about the dynamic of the system based on our results. A further step would be to summarize those hypotheses through state and transition models (Hobbs & Norton 2004; Clewell & Aronson 2007).

Elevation and vegetation

According to our results, most physiognomic types can occur along the whole elevation gradient, while floristic types, although restricted, overlap widely. This means that a given altitudinal belt cannot be named by a single physiognomic or floristic type (see Appendix S5 for a simplified mountain scene).

It is important to highlight that our findings challenge the most established vegetation descriptions in which *S. marginata* and *L. molleoides* woodlands constitute a discrete altitudinal belt at the lower part of the gradient, replaced by the Romerillal belt (shrublands dominated by *B. aliena*) above 1300 m a.s.l.; *sensu* Luti et al. 1979). Present data showed that while the distribution of *S. marginata* types are restricted to lower elevations in line with the traditional description (Luti et al. 1979), types dominated by *L. molleoides* or *V. caven* (C, D, E) have the potential to reach higher elevations than 1300 m a.s.l., and most of our woodland physiognomies showed no elevation restriction. Since neither of our floristic types is dominated by *B. aliena*, our results do not support the existence of the Romerillal belt at a regional scale. The range of elevation between 1300 and 1700 m rather comprises various floristic types and almost all physiognomic types (i.e. seven out of the eight physiognomic types were not significantly restricted along the elevation gradient). This, together with the presence of *P. australis* high mountain woodlands down to 1400 m a.s.l. (Marcora et al. 2008), suggests that woody physiognomic types do not have an elevation restriction in the study gradient. Moreover, it provides further support to local studies reporting successful establishment and growth of woody species, either natives or aliens, along the whole elevation gradient in Córdoba Mountains (Marcora et al. 2008, 2013, 2016; Giorgis et al. 2011a,b; Pais Bosch et al. 2012; Tecco et al. 2016; Urcelay et al. 2017). These findings support the old vegetation description provided by Kurtz (1904), in which all the area below 1700 m a.s.l. belongs to the low-mountain woodland zone.

Taking into consideration the lack of altitudinal restriction of most woody physiognomic types, together with the preference of herbaceous types (1 and 2) for the medium and upper parts of the gradient, we hypothesize that disturbances, interacting with climatic harshness, are the major factors conditioning vegetation physiognomy along the elevation gradient (Cingolani et al. 2008; Giorgis et al. 2013). In this context, the overall decline in growth rate associated with lower temperatures and the increase of frost events at higher elevation (Coomes & Allen 2007) may slow woody recovery after disturbance, as has been demonstrated for *V. caven* in our study area (J. Alinari, unpubl. results). Additionally, the dominance of the grass *F. hieronymi* in floristic types restricted to upper altitudes (A and B) may be explained by the adaptation of this species to cold temperatures (Cabido et al. 2008; Giorgis et al. 2015) and by its shorter life cycle than woody species which may be associated with a fast recovery after disturbance.

All in all, our results indicate important differences between floristic composition and physiognomy in their response to the same gradient, suggesting that both characteristics are partially independent. The floristic restriction along the elevation gradient suggests that the pool of species is mainly conditioned by climate (temperature), which is a relatively stable factor that varies at the regional scale (Woodward 1987; Díaz et al. 1999). In turn, the occurrence of different physiognomic types at all elevations suggests a rapid response of biomass distribution to factors changing at short temporal and spatial scales like fire and grazing (Felfili et al. 2000; Cingolani et al. 2003).

Management implications

Traditionally, managers in the study area assume that native grasslands or shrublands were the potential physiognomy at elevations above 1000–1300 m a.s.l., in which native woodlands were naturally absent. Consequently, they have introduced pine plantations and managed grasslands through the use of grazing and fire (Jobbagy et al. 2013; Cingolani et al. 2014). Recently, it has been demonstrated that pine plantations reduce watershed performance (Jobbagy et al. 2013). Additionally, heavy livestock pressure and high fire frequency on grasslands trigger soil erosion, reducing soil depth and organic matter content, compared with soils protected with woodlands (Renison et al. 2010; Giorgis et al. 2013). Based on our results and previous findings, and taking into consideration that our mountain area is the main reservoir of biodiversity and water in the region (Cingolani et al. 2015), we suggest three main management recommendations.

First, due to the restriction of floristic types along the elevation gradient, we emphasize that any restoration or conservation project should start with a description of all floristic types present at the elevation of interest. Then it would be necessary to hypothesize about the possible successional relationships between different physiognomic types within each floristic type, and between floristic types. These hypotheses could be formalized in a state and transition model (as recommended by Clewell & Aronson 2007). These considerations may help to understand trajectories, and to select resilient and self-sustaining systems of reference (Clewell & Aronson 2007). This point is particularly important for ecosystems like ours having still scarce knowledge about their dynamics.

Second, the system of reference should be selected prioritizing late-succesional physiognomic/floristic types (i.e. dominated by native trees), which are the least common in the area and the most difficult to attain (Zak & Cabido 2002; Clewell & Aronson 2007; Hoyos et al. 2013). In this point we highlight that shrublands may have an important potential for fast recovery and transformation into more mature successional stages. As a consequence, shrubland physiognomic types should receive special focus because they are abundant and could be transformed into valuable woodland types with little effort, by preventing invasions and disturbance by fire and heavy grazing (Clewell & Aronson 2007).

Finally, we recommend special attention to alien species management in any conservation or restoration project. The alternative successional pathway into exotic-dominated woodlands should be prevented through extracting individuals of exotic trees when present. Due to their widespread occurrence, alien plant invasion threatens effectiveness of any landscape management in the region (Hoyos et al. 2010; Giorgis et al. 2011a,b, 2016; Gavier-Pizarro et al. 2012; Salazar et al. 2013; Furey et al. 2014; Giorgis & Tecco 2014; Zeballos et al. 2014; Ferreras et al. 2015).

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MAG, AMC and MC designed the study. MAG, AMC, MC, DEG and PAT contributed to data collection. MAG, MC, JC, FC and DEG contributed plant identification. MAG and AMC carried out data analyses. MAG, AMC and PAT wrote the article with contributions from MC and DEG.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Mean vegetation height.

Appendix S2. Average cover and constancy of the important species.

Appendix S3. Description of the floristic types.

Appendix S4. Description of the physiognomic types.

Appendix S5. A simplified mountain scene.

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