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Understanding clonal plant competition for space over time: a fine-scale spatial approach based on experimental communities

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Abstract

Aims: Competitive interactions are a determinant driver of plant community structure in temperate grasslands. In such dense vegetation cover, competition mostly occurs over free space, which conditions niche availability. Clonal growth determines how plants exploit horizontal space, by (1) exploring and colonizing free patches (guerilla form) or (2) resisting competitors through space consolidation (phalanx form), with possible intermediate strategies. Few studies have explored the dynamics of co-existing plants belonging to different clonal strategies. Models predict that guerilla forms may be advantageous during the early stages of succession, whereas phalanx forms are expected to be better competitors over time. We investigated whether these predictions are true under experimental conditions and explored possible mechanisms that promote clonal plant co-existence.

Location: Experimental garden of the University of Rennes 1, France.

Methods: We set up a large-scale mesocosm, in which we manipulated different mixtures of three clonal growth forms (guerilla, intermediate and phalanx) over 5 yr (2009–2014), which impeded all types of reproduction other than clonal spread of the initial planted individuals. We analysed the spatio-temporal dynamics of the communities using linear mixed models to compare the change in relative cover and spatial association (differentiating between associations with similar and different species) for each clonal form.

Results: Guerilla forms dominated the early community, but decreased in dominance at later stages, at which point intermediate forms benefitted. Furthermore, guerilla forms were more likely to co-occur with other guerrillas, with this pattern remaining consistent over time. In contrast, and contrary to our expectations, phalanx forms had the lowest cover throughout the experiment, and exhibited clear segregation from intermediate or other phalanx species. Intermediate growth forms between guerilla and phalanx were the most variable over time, displaying both consolidative and explorative patterns depending on the clonal forms of the other species which they coexisted with, suggesting plastic variation in their traits.

Conclusions: Our results highlight the key role of clonal forms in driving competitive interactions and, hence, determining the spatio-temporal dynamics of grassland communities.

Introduction

Competitive interactions are a determinant driver of plant community structure in temperate ecosystems, conditioning plant species co-existence and plant community dynamics over time (Tilman 1981; Connell 1983; Goldberg & Barton 1992). A large body of literature has already described this successional dynamic process (Connell & Slatyer 1977; Rees et al. 2001); however, the underlying mechanisms have yet to be elucidated. One important

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mechanism that has been identified is the trade-off between the ability of species to explore and to exploit environmental niches (Tilman 1994). Species performance is promoted during the early successional stages by traits related to colonization (e.g. long-distance dispersal, high reproductive rate), whereas traits related to exploitation (e.g. high specific leaf area) supporting competitive ability are important during the later stages (Kahmen & Poschlod 2004; Fukami et al. 2005). This competition–colonization theory has been confirmed for annual plant communities (Turnbull et al. 1999, 2004), but has not been tested on perennial communities, which become more common during the later stages of ecological succession.

Vegetation cover in grassland ecosystems is dense, resulting in intense competition for resources distributed over space. Therefore, competition for space increases the role of traits linked with space pre-emption in the community dynamics. These traits usually enable species to form a physical barrier that prevents other species from colonizing the area they already occupy. In grassland plant communities, where most species are clonal (van Groenendael & de Kroon 1990) and where sexual recruitment is low (Harper 1977), space pre-emption mostly depends on clonal traits (Herben et al. 1994; Gough et al. 2001). Thus, clonal growth is a key determinant of plant competitive interactions, notably because of its effect on plant spatial patterns (Benot et al. 2013) which, in turn, affect the likelihood of encountering plants with contrasting competitive abilities and, consequently, community dynamics (Murrell et al. 2001, 2002). Clonal growth forms have been described according to their responses in the presence of competitors, with two opposite extremes, classically referred to as the phalanx and guerilla forms (Lovett-Doust 1981). Phalanx species are characterized by clumped growth, conferring strong resistance to the invasion of competitors, whereas guerilla species display strong lateral spread ability that allows them to quickly forage for and colonize free spaces (Slade & Hutchings 1987; Sutherland & Stillman 1988; de Kroon & Hutchings 1995). Based on the competition–colonization theory along ecological succession, guerilla species should dominate the plant community in the short term, but should then be progressively out-competed by phalanx species, which are better exploiters (Gough et al. 2001). Empirical data (Schmid & Harper 1985; Humphrey & Pyke 1998) and modelling studies (Bell 1984; Sutherland & Stillman 1988; Schmid 1990) support this prediction. However, these studies did not control for other factors, such as seed production or external colonization of the community, which can have a profound effect on community dynamics.

In herbaceous plant communities, where species of different clonal growth forms tend to grow together, such theoretical successional dynamics may be modulated by differences in clonal growth between co-existing species. Benot et al. (2013) demonstrated that plant spatial patterns within a community are dependent on the clonal strategies of mixed competitors, suggesting that the characteristics of competing neighbours is a central component in the spatial assemblage of clonal plant communities. A common framework in community assembly theorizes that spatial co-existence in competitive communities is the result of limiting similarity processes and competitive hierarchies (Chesson 2000; Mayfield & Levine 2010). According to limiting similarity, species that present similar traits are expected to compete more intensely among themselves than with different species (i.e. competition relatedness hypothesis; Cahill et al. 2008), promoting the co-existence of species with different traits. Thus, we may expect that both guerilla and phalanx species are able to co-exist throughout community succession. Alternatively, competitive hierarchy theorizes that species with the best competitive ability present similar traits and are able to displace other species, favouring the co-existence of species with similar traits. Therefore, the dominance of either guerilla species at the early stages of succession or phalanx species at the latter stage of succession should be enhanced. At a very local scale (i.e. within a few centimetres surrounding a given plant shoot), limiting similarity should promote spatial segregation between species with similar trait values (i.e. strong segregation between similar clonal growth forms), while competitive hierarchy should favour segregation between species with different traits (i.e. strong segregation between different clonal growth forms). However, the local segregation of space may also depend on the clonal growth form of the species itself, as the long spacers between ramets of guerilla forms allow infiltration in the surrounding vegetation (i.e. promote interspecific contacts), whereas the short spacers of phalanx forms impede the establishment of other species (i.e. promote intraspecific contacts; Lovett-Doust 1981). Thus, patterns of local segregation are expected to be less pronounced for guerilla forms, which are expected to co-occur locally more with other forms, than for phalanx species, which are expected to exhibit a high level of local segregation.

Through an experimental study using mesocosms, we analysed how community spatial dynamics are influenced by different initial compositions of clonal plant growth forms. Specifically, we considered three groups of species with contrasting clonal forms: one group specialized in the colonization of free space (guerilla forms), one group specialized in the consolidation of occupied spaces (i.e. with the ability to form a physical barrier preventing the colonization by other species of the area they occupy: phalanx forms) and one group that was intermediate between the two extremes (intermediate forms). We also investigated how spatial dynamics are modulated by the type of clonal

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strategies present in the plant community. We tested the following hypotheses: (1) along the successional dynamics, guerilla and phalanx strategies should dominate the early and the late stages, respectively; (2) competition for space (reflected in local spatial segregation) should be promoted by phalanx species, which would minimize interspecific contacts, whereas guerilla species would maximize interspecific contacts. This process may become more pronounced over time as space availability decreases. Finally, (3) community spatial dynamics should be influenced by the strategies present in the community, and depend on the specific process driving community spatial assembly. If limiting similarity is operating, competition for space should be higher between species of similar clonal growth form as co-existence is favoured between species with different traits. Furthermore, spatial segregation over time should be more pronounced in communities with similar growth forms (e.g. effect will be higher in communities with guerilla and intermediate forms than in communities with guerilla and phalanx forms). Alternatively, if competitive hierarchy is operating, competition for space should be higher between species of different clonal growth forms as the species with the most competitive clonal traits will impede the establishment of less competitive ones, and spatial segregation over time should be more pronounced in communities with contrasted growth forms (e.g. effect will be higher in communities with guerilla and phalanx forms than in communities with intermediate forms).

Methods

Experimental design

The study was conducted in the experimental garden of the University of Rennes 1, France. Experimental plant communities were established in 2009, including three groups of four species from three clonal growth forms with different space colonization–consolidation capacities. These species are typically found in local semi-natural pastures. The first group included guerilla species (G), specialized in space colonization (*Elytrigia repens* L., *Agrostis stolonifera* L., *Holcus mollis* L. and *Ranunculus repens* L.). The second group included phalanx species (P), specialized in the consolidation of the space they occupy (*Lolium perenne* L., *Dactylis glomerata* L., *Holcus lanatus* L. and *Centaurea nigra* L.). The third group was called intermediate (I), and included species that are not as specialized in colonization or consolidation as the former two groups (*Brachypodium pinnatum* L., *Festuca rubra* L., *Agrostis tenuis* Sibth. and *Anthemis nobilis* L.). The species were classified into the three groups depending on their architecture (differences in their spacer lengths, with guerilla species presenting longer spacers while phalanx species presented the shortest; Table 1; Benot et al. 2013).

In May 2009, seven experimental plant assemblages were established that included all possible combinations of the three clonal groups. Specifically, there were three assemblages composed of the four species of the same clonal group (G, P and I), three assemblages composed of the eight species belonging to two different clonal groups (G-I, G-P and I-P), and one assemblage composed of the 12 species belonging to the three clonal groups (G-I-P). In this way, it was possible to compare the response of each clonal growth form depending on the other clonal forms that co-existed in the assemblage. Each experimental plant assemblage was replicated eight times in culture plots of $1.3 \times 1.3 \times 0.25$ m to produce a total of 56 plots, and replicates were positioned at random within the experimental garden.

Within each plot, 48 clonal fragments were planted in 2009, with 16 cm separation from each other, following a hexagonal pattern (Birch et al. 2007). Each clonal fragment was composed of one mature ramet (i.e. an erect shoot, its leaves and roots; Harper 1977) with one connected spacer for species from G and I clonal groups, and of three joined ramets forming a tuft for species from P group (i.e. spacers were almost nonexistent). The same number of clonal fragments was used for all species present in each experimental assemblage (i.e. 12 for each species in G, I and P; six for each species in G-I, G-P and I-P; and four for each species in G-I-P) and their position in the culture plot was set at random. To avoid the effects of soil heterogeneity, the substrate was homogeneous within and among all culture plots, and was composed of 20% sand and 80% ground soil. In addition, to isolate the effect of clonal growth from the possible effect of seed dispersal, all mature flowers were cut off each year in May–Jul, following plant species phenology, and weeds were regularly removed manually. Above-ground vegetation was mown to 10 cm once a year in late Sept to allow all species to complete their growth period and avoid important regrowth after mowing before winter, because it generates litter that may impede the development of some species.

Plant mapping

In 2010, 2012 and 2014, the cover and spatial distribution of all species within each culture plot was recorded using a square lattice of 80×80 cm centred on the culture plot. In this way, any possible edge effect was minimized. The square lattice was divided into 5×5 cm cells ($T = 256$ cells in total) and the presence/absence of each species within each cell was recorded. A species was considered to be present when a ramet was rooted in the cell. The cell size was selected as it is larger than a single ramet but smaller than a clonal fragment, and corresponded to the scale at which grassland plants are likely to interact (Purves &

Table 1. Classification of species representing each clonal growth form. Mean SL and Max SL correspond to mean (±SE) and maximum spacer length in centimetres, respectively, calculated from measurements on 20 clonal fragments of each species randomly sampled from grasslands.

Guerilla Species	Mean SL (cm)	Max SL (cm)	Intermediate Species	Mean SL (cm)	Max SL (cm)	Phalanx Species	Mean SL (cm)	Max SL (cm)
Elitrygia repens	2.78 (±0.11)	4	*Brachypodium pinnatum*	1.03 (±0.05)	1.5	*Lolium perenne*	0.28 (±0.03)	0.7
Agrostis stolonifera	7.95 (±0.53)	14.5	*Festuca rubra*	0.87 (±0.09)	1.9	*Dactylis glomerata*	0.51 (±0.04)	0.8
Holcus mollis	4.03 (±0.23)	6	*Agrostis tenuis*	2.62 (±0.12)	3.5	*Holcus lanatus*	0.28 (±0.02)	0.4
Ranunculus repens	14.98 (±0.7)	21.3	*Anthemis nobilis*	1.22 (±0.06)	1.7	*Centaurea nigra*	0.44 (±0.04)	0.8

There is a significant effect of clonal growth form in spacer length (ANOVA: $F = 125.6$, $P < 0.001$).

Law 2002). Within plots, the square lattice was positioned in the same way on every sampling date to ensure that data were comparable over time.

Clonal growth form performance

To assess the effect of clonal forms present in the plant community in the performance of each clonal form over time, the change in relative cover for each species i in each year t was calculated within each culture plot as follows: $\Delta\text{Cover}_{i,t} = \frac{\text{Cover}_{\text{obs } i,t} - \text{Cover}_{\text{exp } i,t}}{\text{Cover}_{\text{exp } i,t}}$ (Benot et al. 2013). The observed relative cover ($\text{Cover}_{\text{obs } i,t} = \text{Abundance}_{i,t}/\text{Abundance}_t$) was the number of cells in which species i appeared in year t ($\text{Abundance}_{i,t}$) divided by the sum of the abundance of all species within the plot in year t ($\text{Abundance}_t = \sum_{j=1}^{S} \text{Abundance}_{j,t}$, where S is the initial number of species within the plot). The expected relative cover ($\text{Cover}_{\text{exp}i,t}$) was the value expected under the assumption of equal colonization of space among species ($\text{Cover}_{\text{exp } i,t} = 1/S$). Positive values of $\Delta\text{Cover}_{i,t}$ indicated dominance in species cover in the plant community, while negative values indicated cover values that were lower than expected (a $\Delta\text{Cover}_{i,t} = -1$ indicated the total disappearance of the species from the plot).

Clonal growth form spatial association pattern

The local spatial association pattern of each species in each year was evaluated with three indices according to the spatial co-occurrences of the species with other species present in the culture plot ($co_{ij,t}$, number of cells in which species i co-occurred with species j in time t). First, the general spatial association pattern represented how species i co-occurred with all other species in the culture plot, regardless of their clonal growth form (Fig. 1). This index was calculated as $A_{i,t} = \frac{\text{CO}_{\text{ob si},t} - \text{CO}_{\text{exp } i,t}}{\text{CO}_{\text{exp } i,t}}$, where the observed number of co-occurrences ($co_{\text{ob s } i,t}$) was the total number of times in which species i appeared in the same cell with each of the other species ($co_{\text{obs}i,t} = \sum_{j=2}^{S} co_{ij,t}$). The expected number of co-occurrences ($co_{\text{exp}i,t}$) was the expected number of co-occurrences based on the abundances of the species ($co_{\text{exp } i,t} = \text{Abundance}_{\text{obs } i,t} \cdot \sum_{j=2}^{S} \text{Abundance}_{\text{obs } j,t}/T$). Negative $A_{i,t}$ values indicate that species i co-occurred less than expected in the same cells with other species, indicating that it segregated locally from other species, while positive values indicated that it strongly co-occurred (Saiz & Alados 2012). Then, intra-group ($A_{\text{intra } i,t}$) and inter-group association ($A_{\text{inter } i,t}$) were calculated using a similar method to $A_{i,t}$, but by only considering the co-occurrences with species belonging to the same clonal group ($A_{\text{intra } i,t}$), or to different clonal groups ($A_{\text{inter } i,t}$; Fig. 1). These two indices represented the spatial association between one species and other species with similar or different clonal growth forms, respectively. In this way, it was possible to identify whether community spatial dynamics changed depending on the clonal strategies present in the culture plots.

Statistical analyses

For each clonal group, the significant effects of plant assemblage on all of the four indices ($\Delta\text{Cover}_{i,t}$, $A_{i,t}$, $A_{\text{intra } i,t}$ and $A_{\text{inter } i,t}$) were evaluated with linear mixed models (ANOVA), including experimental plant assemblage and year as fixed effects, and year nested within the culture plot as a random effect. Although our data set did not fulfil normality conditions in all tests, we decided to use ANOVA as they are sufficiently robust to lack of normality when data sets are large enough (in our case, $n > 250$ for all tests; Lix et al. 1996). For the $A_{\text{inter } i,t}$, the communities where only one clonal growth form was present (G, I and P) were not taken into account, as it was not possible to calculate the spatial association between different clonal growth forms. As we were specifically interested in the effect of the assemblage for each growth form and species identity was nested within assemblage, we did not include species identity in our models. To select the model that best described our data, we calculated one model for each of the possible combinations of the explanatory variables (assemblage × year; assemblage + year; assemblage; and year), and we selected the model that presented the lowest

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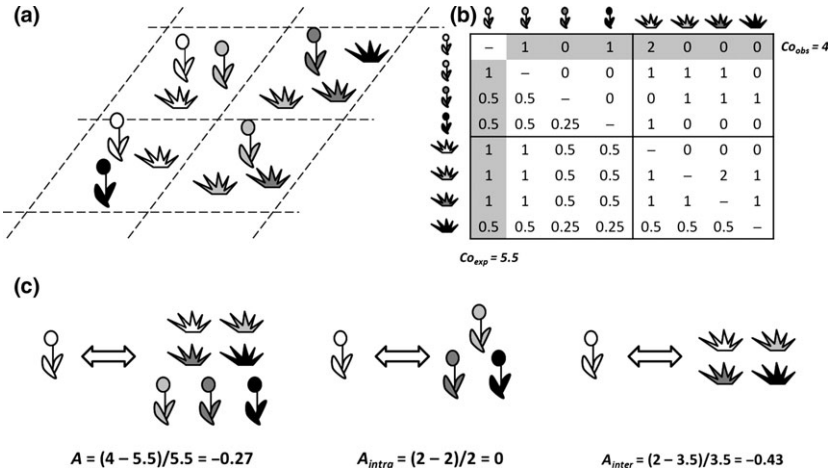

Fig. 1. Calculation of local spatial association patterns in each culture plot. Example of an experimental community with two clonal growth forms. Each combination of shape and grey nuances represents one species, and species with same shape have the same clonal growth form. Each experimental plot is divided into cells (**a**) and the co-occurrences of all species with all species are recorded (**b**). Values above diagonal are the observed co-occurrences while values below diagonal are expected co-occurrences based on species abundances. With co-occurrence data, different association indices (**c**) are calculated according to the particular spatial association pattern we are interested in. For example, for a given species *i* the data highlighted in grey are used to calculate its general association pattern with respect to all other species in the community ($A_{i,t}$), species belonging to the same clonal group ($A_{\text{intra } i,t}$), or species from a different group ($A_{\text{inter } i,t}$). Note that $A_{i,t}$ is not the sum or the average of $A_{\text{intra } i,t}$ and $A_{\text{inter } i,t}$.

AIC as the best (Zuur et al. 2009). To study the differences between the levels of the significant fixed effects, we made different post-hoc analyses depending on the presence or absence of significant interaction in the model. If significant interaction was found, Tukey tests for Honest Significant Differences (Tukey HSD) were completed, including the effect of the residuals in the calculation of the significant differences using R. Specifically, we tested whether there were significant differences between years for each specific experimental assemblage, and whether there were significant differences between experimental assemblages for each specific year. When interaction was not significant, post-hoc Tukey HSD was calculated to assess significant differences between factor levels. All indices were calculated with R software (R Foundation for Statistical Computing, Vienna, AT), linear-model ANOVAs were calculated using *nlme* package, and post-hoc tests were performed using *phia* package.

Results

Clonal growth form performance

Regarding the changes in relative cover ($\Delta\text{Cover}_{i,t}$), we found a significant effect of the interaction between plant assemblage and year on the performance of all three clonal groups (Table 2). Specifically, species from the guerilla group presented positive values of $\Delta\text{Cover}_{i,t}$ (Fig. 2 top), indicating that they tended to cover all of the available space. Post-hoc tests did not show changes in guerilla cover with time for any of the plant assemblages, but there were differences between assemblages in different specific years (Table 3, Fig. 2 top). Thus, in 2010, guerilla relative cover was higher when co-existing with the other two groups (G-I-P) compared to when grown alone (G; Fig. 2). The phalanx group showed overall negative $\Delta\text{Cover}_{i,t}$ values, particularly when co-existing with guerillas, representing their inability to cover space (Fig. 2 bottom). The only variation of phalanx cover through time was recorded when co-existing with the intermediate clonal group (I-P), with a decrease in $\Delta\text{Cover}_{i,t}$ (Table 3, Fig. 2 bottom). Finally, species from the intermediate clonal group presented negative $\Delta\text{Cover}_{i,t}$ values in all experimental assemblages during 2010, showing low colonization at the beginning of succession (Fig. 2 middle). However, in the presence of phalanx species (I-P and G-I-P assemblages), the cover of the intermediate group significantly increased through time (Table 3, Fig. 2 middle).

Clonal growth form spatial association pattern

To assess the competition for space of each clonal group and how it changed according to its neighbouring clonal growth forms, we used the general spatial association pattern ($A_{i,t}$) and the specific association of species from the same or different clonal groups ($A_{\text{intra } i,t}$ and $A_{\text{inter } i,t}$, respectively). Species from the guerilla clonal group did not present a segregated spatial pattern ($A_{i,t} \approx 0$, co-occurrence with other species equals the expectations considering their abundance). Furthermore, this spatial pattern remained similar throughout the experiment (no

Table 2. Results of the linear model ANOVAs for the effect of plant community assembly, year and the interaction of these two variables on the performance and spatial association indices.

Clonal Group	Index	*n*	Plant Assemblage	Year	Plant Assemblage x Year
Guerilla	$\Delta Cover_{i,t}$	384	$F = 61.15$***	$F = 26.24$***	$F = 14.15$***
	$A_{i,t}$	344	-	-	-
	$A_{intra\ i,t}$	344	$F = 1.47$ n.s.	$F = 8.67$***	$F = 6.22$***
	$A_{inter\ i,t}$	357	-	-	-
Intermediate	$\Delta Cover_{i,t}$	384	$F = 24.34$***	$F = 118.37$***	$F = 14.87$***
	$A_{i,t}$	281	$F = 9.54$***	$F = 21.31$***	$F = 4$**
	$A_{intra\ i,t}$	281	-	$F = 12.15$***	-
	$A_{inter\ i,t}$	255	$F = 24.84$***	-	-
Phalanx	$\Delta Cover_{i,t}$	384	$F = 21.69$***	$F = 41.29$***	$F = 18.11$***
	$A_{i,t}$	315	$F = 18.6$***	$F = 3.85$*	$F = 3.18$**
	$A_{intra\ i,t}$	315	-	-	-
	$A_{inter\ i,t}$	308	-	-	-

n, number of data employed in the analysis (4 species/culture plot × 8 culture plots/experimental assemblage × 4 experimental assemblage/year × 3 yr = 384); $\Delta Cover_{i,t}$, changes in relative cover; $A_{i,t}$, general spatial association pattern; $A_{intra\ i,t}$, association with species from the same clonal group; $A_{inter\ i,t}$, association with species from different clonal groups. Missing values (-) indicate that those factors were not included in the best model (with the lowest AIC). Differences in *n* values were due to the disapearance of some species from the culture plots during the experiment. Results in bold indicate significant effects. n.s. $P > 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

significant effect of year) and independent from the other clonal growth forms present in the assemblage (Table 2, Fig. 3 top). However, plant assemblages and year had a significant effect on associations with species from the same clonal groups ($A_{intra\ i,t}$ responded to assemblage × year; Table 2). Specifically, segregation among guerilla species increased with time when co-existing with phalanx species (Table 3, Fig. 4 top).

Phalanx species were strongly segregated from other forms, which was indicated by the low negative values of $A_{i,t}$, $A_{intra\ i,t}$, and $A_{inter\ i,t}$ (Figs 3–5 bottom). Specifically, their spatial association pattern ($A_{i,t}$) depended on the species assemblage and time (Table 2). In general, phalanx species were less segregated with other species when guerilla species were also present (Fig. 3 bottom). When phalanx species co-existed with intermediate species, spatial segregation was high at the beginning of the experiment and decreased with time (Table 3, Fig. 3 bottom). In comparison, there was no significant effect of time or species assemblage on the spatial association pattern between phalanx species ($A_{intra\ i,t}$), nor in the spatial association pattern between phalanx species and other clonal groups ($A_{inter\ i,t}$).

Species in the intermediate group showed the highest variability in spatial pattern ($A_{i,t}$) between years, and were highly influenced by the clonal forms with which they co-existed (Table 2, Fig. 3 middle). Specifically, in 2010 the intermediate species were less segregated when guerilla species were present in the assemblage (G-I and G-I-P mixtures) compared to when mixed with phalanx species (I-P) or alone (I). For both of these latter assemblages, intermediate species became less segregated with time (no differences in $A_{i,t}$ were found between species assemblages in 2014), with a similar result being obtained for phalanx species in I-P assemblages (Fig. 3 middle). These changes were due to changes in their spatial association with similar and different clonal forms. Specifically, the $A_{intra\ i,t}$ of intermediate species became less segregated through time in all the community assemblages (Table 2, Fig. 4 middle), with this group showing a significant difference in how they associate with guerilla ($A_{inter\ i,t}$ close to zero, no segregation) and phalanx species (lower $A_{inter\ i,t}$, high segregation; Fig. 5 middle).

Discussion

Our experimental study clarified the role that clonal growth forms play in the performance of plant species, and also provided evidence of the modulating effect of neighbouring clonal growth forms in spatial associations among species over time. Competition for space was dependent on clonal growth forms, but was not clearly related to any of the theoretical community structuring processes (*i.e.* limiting similarity vs competitive hierarchy). These results confirm that competition for space is critical in the structuring of clonal plant communities, and demonstrate the necessity of considering the different clonal growth forms that co-exist in a given environment to understand the mechanisms that regulate the actual assemblages of plant communities.

Effect of clonal growth form on plant performance over time

Our results partially support our initial prediction, with guerilla (G) species being dominant from the first year in

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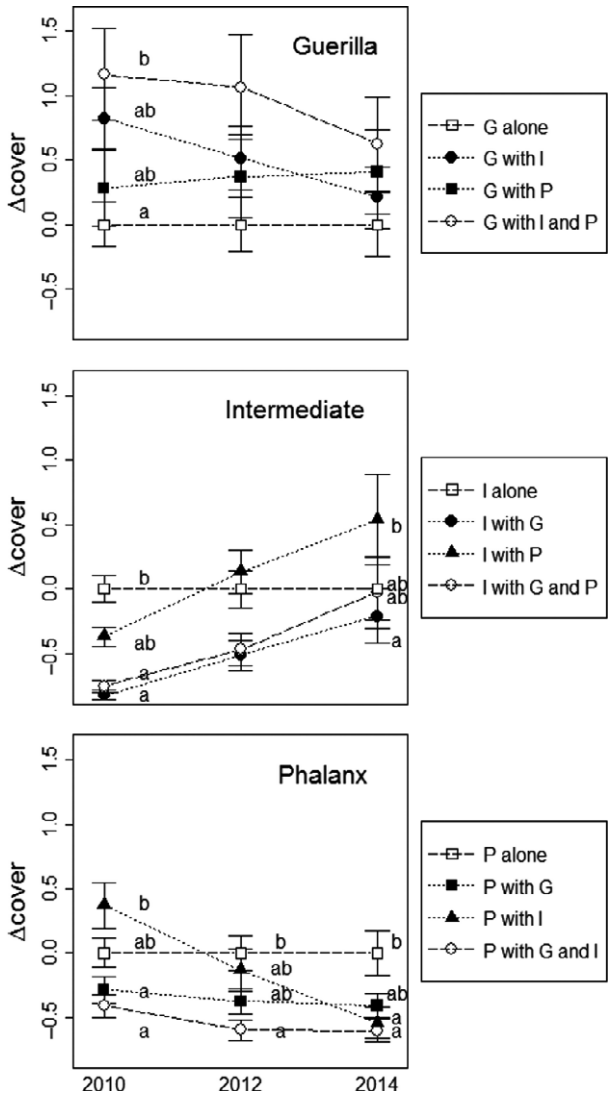

Fig. 2. Effect of plant assemblage and year on the performance of clonal forms. G, Guerilla; I, Intermediate; and P, Phalanx clonal growth forms. The *x*-axis includes the time periods when data were collected. White circles represent G-I-P community, while white squares represent the community where there was only one clonal group present. Black squares represent G-P community, black circles G-I community, and black triangles I-P community. Values below and above 0 indicate that the relative abundance of species from that clonal group was, respectively, lower and higher than expected. All clonal forms present a significant interaction between plant community assemblage and year. Letters indicate significant differences between plant assemblages for each specific year.

all of the experimental communities, and intermediate (I) species increasing their relative cover with time. However, contrary to our expectations, phalanx (P) species consistently presented the lowest relative cover, which did not increase through time. According to the competition–colonization trade-off (Tilman 1994), plants specialized in space consolidation (phalanx) should become increasingly dominant through time at the expense of best colonizers (guerrilla; Kahmen & Poschlod 2004; Fukami et al. 2005). More importantly, our study showed that clonal form performance is influenced by time and the other forms present in the species assemblages. Specifically, the presence of guerilla species resulted in the underperformance of other forms, particularly at the beginning of the experiment, while intermediate forms increased their relative cover through time when phalanx forms were present in the assemblage. One possible explanation for the dominance of colonizers in the experiment can be the founder control effect. Founder control happens if the dominant species in a competitive interaction is the species that was the most abundant at the beginning (Levin et al. 2009). In clonal plant communities, this phenomenon may occur if the first arriving species capture space very effectively and are able to withstand competition from other forms that occupy space more slowly (Svensson et al. 2005). Thus, space colonization by phalanx species was hampered where guerillas and intermediates were already settled, which even led to the loss of phalanx cover through time to the benefit of intermediate forms. The same phenomenon happened to intermediate forms, which had low cover in the assemblages with guerillas (even though, as expected, they increased their relative cover through time). Another possible explanation is that our experimental time period (5 yr) was not long enough to obtain empirical evidence about the progression of phalanx species. For example, Prach & Pyšek (1994) found that after 10 yr of succession in an environment without disturbance, guerilla forms were still more dominant than phalanx forms. Therefore, it is possible that more time is required for phalanx species to out-compete other forms in the community.

Effect of clonal growth form on plant spatial associations over time

The values of spatial segregation recorded in our experiment for the different clonal growth forms were consistent with their position along the colonization–consolidation strategies. Indeed, we predicted that clonal forms specialized in consolidating space (phalanx) should promote spatial segregation, while colonizers (guerilla) should have a less segregated pattern. This result extends the hypothesis for the existence of competitive hierarchies in plant communities (where competition is usually measured as abundance or biomass; Keddy et al. 1994; Fraser & Keddy 2005) to include competition for space (in our case, phalanx > intermediate > guerilla). This result also provides further evidence supporting the relationship between spatial patterns and biotic interactions among sessile organisms (Herben & Hara 1997; Murrell et al. 2001; Wiegand

Table 3. Post-hoc tests for significant differences between years on the performance and spatial association indices.

Clonal Group	Plant Assemblage	$\Delta Cover_{i,t}$	$A_{i,t}$	$A_{intra\ i,t}$
Guerilla	G	n.s.	–	n.s.
	G-I	n.s.	–	n.s.
	G-P	n.s.	–	2010 > 2012 > 2014
	G-I-P	n.s.	–	n.s.
Intermediate	I	n.s.	2010 < 2012 < 2014	2010 < 2012 = 2014
	G-I	n.s.	n.s.	2010 < 2012 = 2014
	I-P	2010 < 2012 < 2014	2010 < 2012 < 2014	2010 < 2012 = 2014
	G-I-P	2010 < 2012 < 2014	n.s.	2010 < 2012 = 2014
Phalanx	P	n.s.	n.s.	–
	G-P	n.s.	n.s.	–
	I-P	2010 > 2012 > 2014	2010 < 2012 < 2014	–
	G-I-P	n.s.	n.s.	–

$\Delta Cover_{i,t}$, changes in relative cover; $A_{i,t}$, general spatial association pattern; $A_{intra\ i,t}$, association with species from the same clonal group. Missing values (–) indicate that year was not included in the model with the lowest AIC. Significant differences were evaluated with Tukey HSD pots-hoc tests. n.s. indicates that there were no significant differences between years. $A_{inter\ i,t}$ was not included as year was not significant in any model.

et al. 2003). In this case, competition for space should be driven by the creation of barriers from plant species that impede the establishment of other species, leading to a spatial pattern that is the direct result of competition for space (Humphrey & Pyke 1998; Gough et al. 2001).

The effect of time on spatial dynamics was specific to the particular clonal growth form considered. Guerilla species presented low spatial segregation, and were not affected by time or the types of clonal growth forms present in the assemblage. Clonal plants with guerilla forms have long spacers, and are expected to occupy space very quickly, infiltrating the surrounding vegetation from the early stages of the assemblage and maximizing their contacts with other species (Lovett-Doust 1981). Furthermore, this capacity to infiltrate vegetation resulted in the lower spatial segregation of other forms in assemblages where guerillas were present. In comparison, phalanx species had high spatial segregation, which did not change through time, but only in assemblages where intermediate forms were present. Phalanx species have short spacers, and grow by forming mono-specific clumped tufts with tight tillers that hamper the infiltration of other species, promoting co-occurrence with intraspecifics and segregating other forms (Lovett-Doust 1981). Intermediate species were the most influenced by time, exhibiting a decline in segregation when they grew alone or in an assemblage with just phalanx species. This result contradicted our prediction for increasing segregation through time, and may be due to the active response of clonal forms in response to competitive neighbours (Bülow-Olsen et al. 1984; Schmid 1986). In this case, once all the space in the culture plots was occupied, plant species were obliged to co-occur more often with others forms. Consequently, intermediate forms could have promoted clonal traits that facilitated the local co-existence of species, resulting in a general decrease in community segregation.

Processes driving the spatial dynamics of plant assemblages

Our results only weakly supported limiting similarity and competitive hierarchy processes as being responsible for the successional dynamics in our experimental clonal communities. We found no differences between the assemblages with contrasted (G-P) and similar clonal growth forms (G-I and I-P) for the considered indices. One possible explanation is that we considered a trait involved only in space horizontal occupancy. Limiting similarity is based on the idea that differences in trait values allow the exploitation of non-overlapping parts of the resource (Chesson 2000). Thus, it is possible that in our case differences between spacer lengths did not allow the exploitation of different parts of the resource – space – but only affected how species procure that resource (fast colonization of empty sites vs strong consolidation of the occupied space). Moreover, Herben & Goldberg (2014) recently showed that community assemblage may be driven by limiting similarity or competitive hierarchy depending on the traits being considered. Specifically, the authors suggested that traits related to spatial colonization are related to limiting similarity processes and promote the co-existence of different species. At the same time, traits related to competition for resources are related to competitive hierarchy and promote the co-existence of similar species. When considering the local spatial association between similar and different clonal growth forms, we found no evidence of either process, but we did find that the clonal growth form of the species itself had a strong effect. Specifically, guerilla forms had higher segregation with other clonal forms (phalanx), while phalanx forms were primarily segregated from other phalanx forms. One explanation is that competition for space is not the result of one specific clonal trait; rather, it depends on the capacity of plants to arrive at new sites

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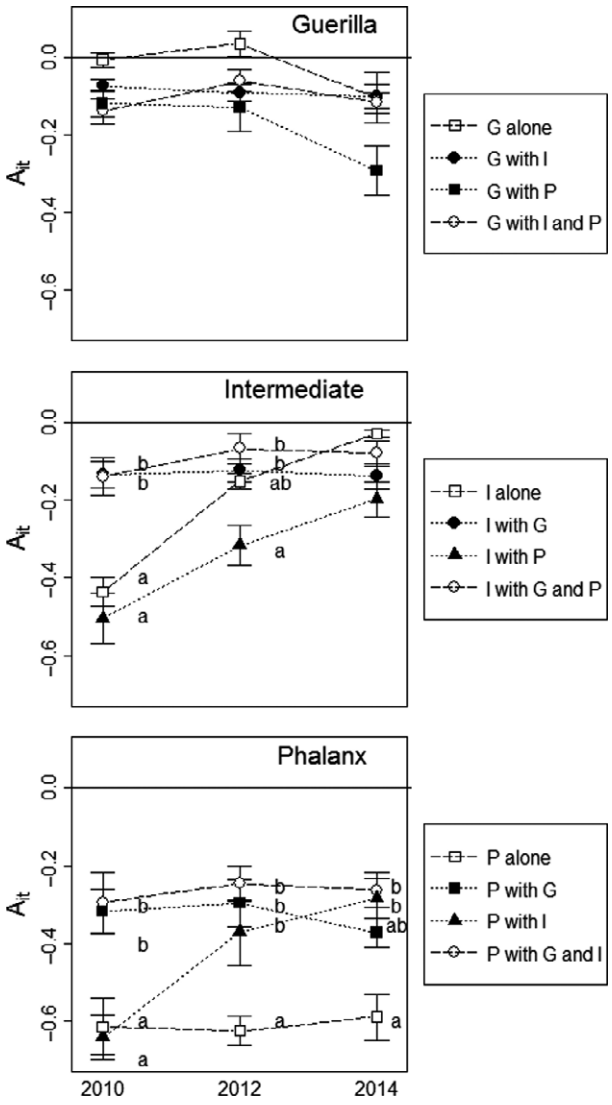

Fig. 3. Effect of plant assemblage and year on the spatial association pattern of clonal forms. G, Guerilla; I, Intermediate; and P, Phalanx clonal forms. The *x*-axis includes the time periods were data were collected. White circles represent G-I-P community, while white squares represent the community where there was only one clonal group present. Black squares represent G-P community, black circles G-I community, and black triangles I-P community. Values below 0 indicate that clonal group was spatially segregated. There is a significant interaction between plant community and year for I and P clonal forms. Letters indicate significant differences between plant communities for each specific year.

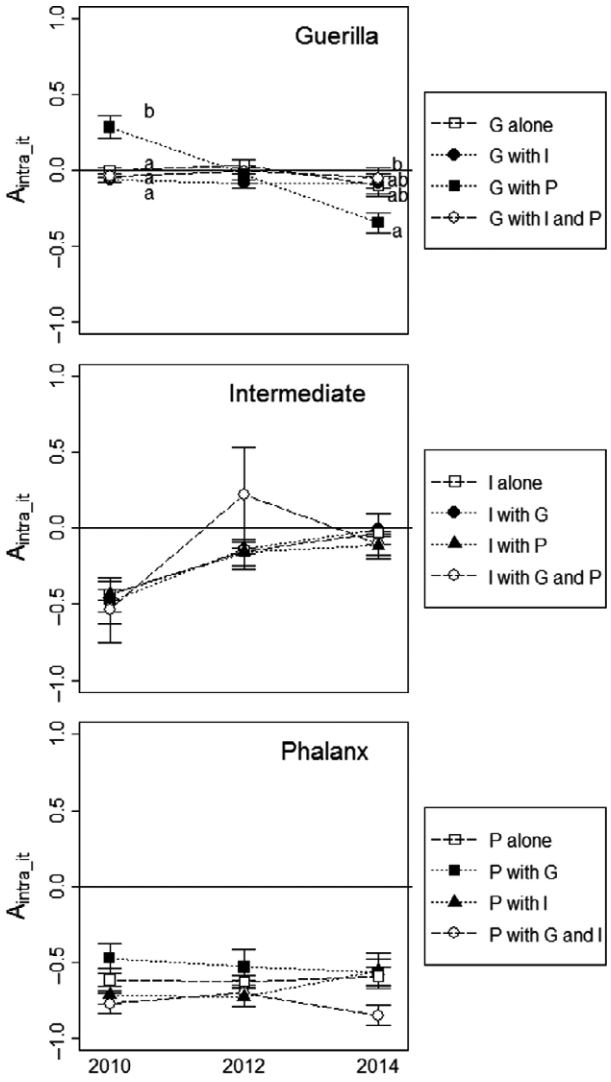

Fig. 4. Effect of plant assemblage and year on the spatial association pattern among species from the same clonal form. G, Guerilla; I, Intermediate; and P, Phalanx clonal forms. The *x*-axis includes the time periods where data were collected. White circles represent G-I-P community, while white squares represent the community where there was only one clonal group present. Black squares represent G-P community, black circles G-I community, and black triangles I-P community. Values below 0 indicate that species from the same clonal group were spatially segregated. There is a significant interaction between plant community and year for G clonal group. Letters indicate significant differences between plant communities for each specific year.

(colonization), uptake of nutrients and preventing the establishment of other species (consolidation). Thus, as many traits are involved, both processes may occur simultaneously, not being able to infer a clear pattern. The species considered in the study may display differences in other traits than those considered for establishing the clonal groups, obscuring the identification of the underlying processes. Novel analyses considering multiple clonal and non-clonal traits simultaneously (Blonder et al. 2014) may be required to unveil the complexity behind spatial dynamics, and may help to elucidate the specific processes that influence each trait.

Interestingly, the intermediate forms, in contrast to guerilla and phalanx forms, were significantly affected by

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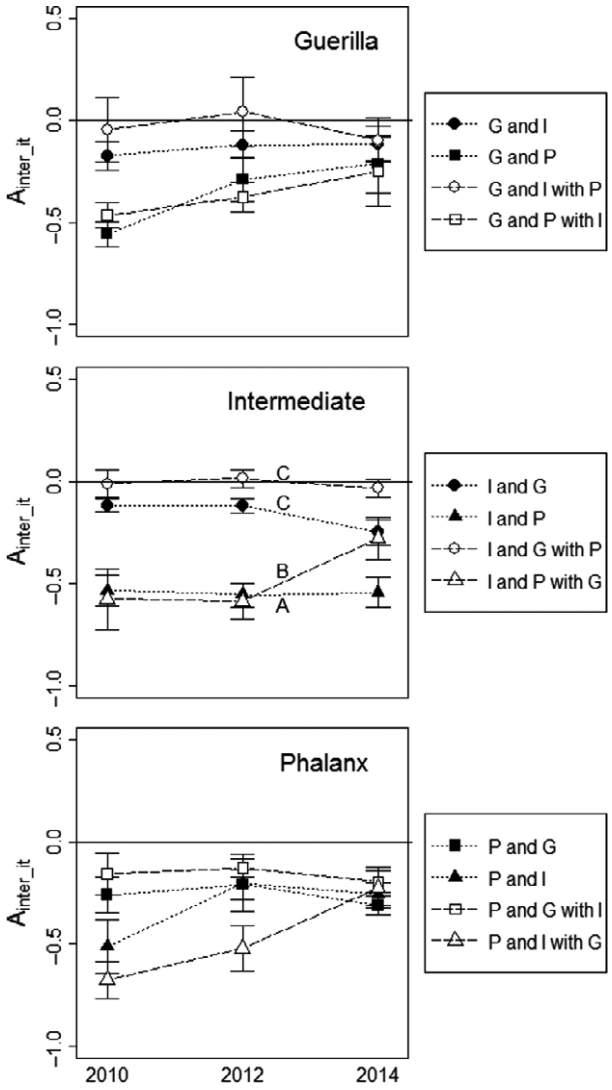

Fig. 5. Effect of plant assemblage and year on the spatial association pattern among species from different clonal forms. G, Guerilla; I, Intermediate; and P, Phalanx clonal forms. The *x*-axis includes the time periods where data were collected. Black symbols represent inter-group spatial associations for the communities with two different clonal forms, while white symbols represent communities with three clonal forms. Squares represent G-P spatial association, circles G-I spatial association, and triangles I-P spatial association. Values below 0 indicate that species from different clonal forms were spatially segregated. There is no significant effect of year or the interaction between plant community and year. Thus, capital letters indicate significant differences between plant communities independently of year.

both time and the clonal forms with which they co-existed. These results may be explained by the higher spatial pattern variability of intermediate forms with respect to other clonal forms in response to their neighbour species. Plant species are able to modify their competitive behaviour to minimize competitive interactions and increase their long-term gains (Aphalo & Ballare 1995), favouring or avoiding competition with other species (Novoplansky 2009; Herben & Novoplansky 2010). Studies on the plasticity of clonal traits suggest that guerilla species are more plastic than phalanx ones (Pottier & Evette 2009). However, our results show that the least specialized forms (intermediate species are situated between guerilla and phalanx species in the colonization–consolidation continuum) present the most variable responses in spatial occupancy. Although we did not directly measure individual clonal traits during the time of the experiment, this variability could be linked to a high plasticity in clonal traits (e.g. spacer length) in intermediate species. Thus, intermediate forms presented a spatial pattern that varied from low to high segregation, depending on the clonal growth forms of the other species present in the community. This result, together with the dynamic response of intermediate forms (leading to a decrease in their spatial segregation through time), indicates that intermediate forms presented a variable response in our experiment. This variability of intermediate clonal forms may explain their co-existence in natural communities with other more competitive forms, which, in normal conditions, would out-compete them (Tilman 1994). This result supports the importance of the clonal traits plasticity, which has been demonstrated for both traits involved in space colonization and consolidation processes (Turkington 1990; Turkington et al. 1991; Hutchings 1994; Bittebiere et al. 2012; Bittebiere & Mony 2014). Further work is required to survey how clonal traits change over time; however, our results indicate that it is important to consider this variability as a modulating factor when studying the spatial dynamics of assemblage processes.

Conclusion and perspectives

Experimental studies relying on mesocosms allow us to isolate the single effect of variables of interest by controlling environmental variability. Our analysis of the spatial dynamics in clonal plant communities revealed that the dominance of colonizer forms at the beginning of succession impeded the colonization of other forms, which were not able to out-compete the colonizers. Furthermore, neither limiting similarity nor competitive hierarchy appeared to drive competition for space, which strongly depended on the clonal growth form of the species. Competition for space is the result of traits involved in spatial colonization, resource uptake and resistance to the invasion of competitors, with each of these traits being driven by different processes. Thus, to obtain a complete understanding about community spatial dynamics, approaches that consider different traits and processes simultaneously are required. Furthermore, clonal growth forms specialized in a specific strategy (colo-

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nization or consolidation) showed a very consistent spatial pattern through time with different assemblages, while less specialized forms were able to change their pattern dynamically in response to their neighbours. These results show that clonal plants are able to modify how they compete for space, indicating that the plasticity of clonal traits involved in space pre-emption has a major effect on the spatial dynamic of clonal plant communities, and might contribute to the maintenance of diverse clonal strategies in natural plant communities.

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