Vegetation structure of plantain-based agrosystems determines numerical dominance in community of ground-dwelling ants (#17973)

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Vegetation structure of plantain-based agrosystems determines numerical dominance in community of ground-dwelling ants

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In tropics, ants may represent an important part of animal biomass and are known to be involved in ecosystem services, such as pest regulation. Understanding the mechanisms underlying the structuring of local ant communities is therefore important in agroecology. In the humid tropics of Africa, plantains are cropped in association with many other annual and perennial crops. Such agrosystems differ greatly in vegetation diversity and structure and are well-suited for studying how habitat-related factors affect the ant community. We analysed abundance data for the six numerically dominant ant taxa in 500 subplots located in 20 diversified, plantain-based fields. We found that the density of crops with foliage at intermediate and high canopy strata determined the numerical dominance of species. We found no relationship between the numerical dominance of each ant taxon with the crop diversity. Our results indicate that the manipulation of the densities of crops with leaves in the intermediate and high strata may help maintain the coexistence of ant species by providing different habitat patches. Further research in such agrosystems should be performed to assess if the effect of vegetation structure on ant abundance could result in efficient pest regulation.

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Abstract

In tropics, ants may represent an important part of animal biomass and are known to be involved in ecosystem services, such as pest regulation. Understanding the mechanisms underlying the structuring of local ant communities is therefore important in agroecology. In the humid tropics of Africa, plantains are cropped in association with many other annual and perennial crops. Such agrosystems differ greatly in vegetation diversity and structure and are well-suited for studying how habitat-related factors affect the ant community. We analysed abundance data for the six numerically dominant ant taxa in 500 subplots located in 20 diversified, plantain-based fields. We found that the density of crops with foliage at intermediate and high canopy strata determined the numerical dominance of species. We found no relationship between the numerical dominance of each ant taxon with the crop diversity. Our results indicate that the manipulation of the densities of crops with leaves in the intermediate and high strata may help maintain the coexistence of ant species by providing different habitat patches. Further research in such agrosystems should be performed to assess if the effect of vegetation structure on ant abundance could result in efficient pest regulation.

Keywords: ant, dominance, vegetation structure, cultivated plant diversity, plantain

Introduction

In tropics, ants are known to potentially represent the major part of animal biomass (Hölldobler and Wilson, 1990). Moreover, in agrosystems, they are known to be involved in pest regulation and other ecosystem services (Perfecto and Vandermeer, 2006, Philpott and Armbrecht, 2006). Understanding the factors affecting the structure of local ant communities is therefore an important issue in agroecology. The structure of the community may be related to physiological factors (humidity and temperature) and ecological factors (Philpott and Armbrecht, 2006). These ecological factors include, on the one hand, ecological interactions (e.g., foraging interference) and, on the other hand, the habitat-related factors (e.g. nesting sites) which are the focus of the present study.

Previous studies have shown that vegetation may affect the ant communities by affecting habitat structure (Perfecto and Vandermeer, 1996, Vasconcelos et al., 2008, House et al., 2012, Murnen et al., 2013). A common observation of these studies is that habitats that reduce the abundance of a dominant ant species increase ant species richness. Perfecto and Vandermeer (1996) showed that the addition of artificial shade to a tropical agrosystem decreased the abundance of the dominant ant *Solenopsis geminata* F. (Hymenoptera: Formicidae) while it increased the abundance of other ant species. Vasconcelos et al. (2008) found that trees and tall grasses affect ant species composition in savannas of South America; more specifically, they reported that tall grass cover reduced the incidence of the dominant ant species, *Solenopsis substituta* (Santschi) (Hymenoptera: Formicidae). In a study of ants in an agricultural matrix, House et al. (2012) found that species richness and abundance were higher in native woodlands than in pastures or crops but that dominance by ants in the *Dolichoderinae* was higher in pastures or crops than in native woodlands. By manipulating food and nesting site availability, Murnen et al. (2013)

demonstrated that ant community composition is greatly influenced by habitat type, which determines nesting resource availability, while food quantity alone had no effect on community composition.

Ant diets vary within and between subfamilies and genera. Many ants may be mainly omnivorous and opportunistic, while others are specialized for predation, fungus-growing, or herbivory (seeds and nectar) (Hölldobler and Wilson, 1990). Therefore, at the community level, ant diets represent a continuum between herbivory and strict predation (Bluthgen et al., 2003) and are likely to be affected by plant diversity. Scherber et al. (2010) have shown that the effects of plant diversity on abundance and species richness decrease with increasing trophic level and degree of omnivory. Bluthgen et al. (2003) proved through isotope analysis that the dominant ant species with small to intermediate colonies in tree canopies tend to be herbivorous (including feeding on extrafloral and floral nectaries), that the dominant canopy ants with large colonies tend to be omnivorous, and that understorey or ground-dwelling ants tend to display higher trophic levels.

In the humid tropics of Africa, plantains (*Musa* AAB genome) are cropped in association with annual crops (root, tuber, and vegetable crops) and perennial crops (cocoa, coffee, and palm). Because such agrosystems differ greatly in vegetation diversity and structure, they are useful for studying how habitat-related factors affect ant community structure. Using diversified plantain agrosystems in the current study, we (i) determined the dominant and subordinate ant genera in the dry and rainy seasons and (ii) tested the hypotheses that local vegetation structure and plant diversity determine the numerically dominant ant genus.

Methods

Fields, plots, and subplots

We conducted our study in the Moungo department of the Littoral Region of Cameroon (Central Africa) from June 2012 to February 2013. We selected 20 farmer fields near the CARBAP research station (4° 34' 11.33'' N; 9° 38' 48.96'' E; 79 m a.s.l.). All the fields have a young, brown soil derived from a volcanic platform (Delvaux et al., 1989). The climate is humid tropical with a monthly mean temperature ranging from 25.0 to 27.4°C and a mean annual rainfall of 2610 mm. All fields contained plantain crops (*Musa AAB* genome) and a diverse array of other annual and perennial crops. Pesticides and fertilizers are rarely applied in these agrosystems with low inputs.

In each field, we assessed ants and crops in one 12 X 12 m plot, which was subdivided into 25 subplots of 2.4 X 2.4 m. We sampled during two periods: the rainy season (mid-March 2012 to mid-November 2012) and the dry season (mid-November 2012 to February 2013).

Vegetation structure and diversity

For all subplots, we identified all cropped plants, measured their density (number of plants of each species per m^2), and recorded their coordinates with a measuring tape (using subplot corners as a references to minimize error). We classified the plant species into four categories according to the location of their canopies relative to the soil surface: low stratum (height ≤ 2m), intermediate stratum (2m < height ≤ 6m), high stratum (height > 6m), and *Musa* group. For each category, we calculated the density of plants, i.e. the number of plants of a considered category per m^2. Plant diversity at each subplot was assessed by the Shannon Index (Shannon, 1948), which was calculated with the 'diversity' function of the 'VEGAN' R package (Dixon, 2003).

Bait sampling

In each subplot, we measured ant abundance by using 2/3 tuna– 1/3 honey baits. The 2 cm-radius bait was placed in the centre of a white ceramic square tile (30 cm side), which was itself placed at the ground level in the centre of the subplot. Thirty minutes after the baits were deployed, we counted the individuals of different species/morphospecies present on the tile. Samples of all observed species were collected and conserved in 70% alcohol to perform identification to genus according (Fisher and Bolton, 2016) and a morphospecies was assigned to the individual on the basis of morphological specificities. The ants were also recorded according to a 6 point abundance scale (following Andersen, 1997; Parr et al, 2005; Baccaro et al, 2010). We used the same method as in Carval et al. (2016), based on the percentage of bait controlled and on the mean abundance score, to determine dominance We performed bait samples twice for each subplot, during two periods: the rainy season (mid-March 2012 to mid-November 2012) and the dry season (mid-November 2012 to February 2013).

Dominant, subdominant and subordinate ants

Following Baccaro et al. (2010) and similarly to Carval et al. (2016), we combined three numerical and behavioral criteria of dominance to determine dominant, subdominant and subordinate ants at the genus level. The dominant (respectively subdominant) ants were considered as those that were recorded in >10% of all baits, controlled >25% (respectively > 10%) of baits where they occurred, and with a mean abundance score (i.e. the sum of the abundance scores for the genus at all baits divided by the number of baits at which the genus was present) of >3.5 (respectively > 3). All other genus that did not meet all these criteria was considered as subordinate species.

We assessed the influence of the season (dry, rainy) on the abundance of each genus by using Poisson generalized linear models.

Effect of vegetation strata on numerical dominance of ants

For each subplot, we attributed rank values for each ant genus according to their respective abundances (Parr and Gibb, 2010). Species with the rank of one was considered as the numerically dominant genus at the subplot scale. Then, we used multinomial logit model to assess the effect of plant diversity and of the density of each stratum on the probability that an ant genus was numerically dominant. We used likelihood ratio tests (LRTs) to select the best model by removing non-significant parameters in a backwards-stepwise process. The selection procedure was continued until a model was found in which all effects were significant (Zuur et al., 2009). Multinomial models were estimated using the 'VGAM' package (Yee, 2010).

All statistical analyses were performed with R 3.3.1 (R Development Core Team, 2016) and with an alpha level of 0.05.

Results

Dominant, subdominant, and subordinate ants

At the exception of *Axinidris* sp. which was absent at baits in the rainy season, all taxa were present in relatively high proportion ranging from 10% to 43% (Table 1).. *Pheidole* spp. were identified as the dominant genus because they combined a large proportion of controlled baits and a high mean score abundance (Table 1). *Axinidris* sp. was identified as a subdominant species because it combined a moderate proportion of controlled baits and a high mean score abundance (Table 1). All other species or genus were considered as subordinate (Table 1).

Abundance of each taxon was not significantly affected by the season, except for *Axinidris* sp. which was absent at baits in the rainy season (Fig. S1 & S2, Table S1). Frequencies of numerical dominance were similar in the rainy season and dry season (Fig. 1).

Effect of vegetation strata on numerical dominance of ants

We collected 31 plant species, which we grouped into four vegetation strata (Table 2). The probability of dominance of each ant taxa was not significantly affected by the density of plants in the low and *Musa* strata but was significantly affected by the density of plants in the intermediate and high strata (Table 3). The dominance of *Pheidole* spp., *Monomorium* spp., and *Tetramorium sp*. was negatively correlated with the density of plants in the intermediate and high strata, whereas the dominance of *Paratrechina longicornis*, *Camponotus* spp., and *Axinidris sp*. was positively correlated with the density of plants in the intermediate and high strata (Fig. 2). The probability of dominance of each ant taxa was not significantly affected by plant diversity (Table 2).

Discussion

We found that ants of the *Pheidole* genus were the numerically dominant ants in our study fields. Abera-Kalibata et al. (2007) also found that *Pheidole* spp. were the most abundant ants in banana fields in Uganda. We observed similar frequencies of numerical dominance for *P. longicornis*, *Camponotus* spp., and *Monomorium* spp. These results also agree with the literature in that ants of the *Camponotus* genus are considered ubiquitous subordinate ants that may numerically dominate arboreal vegetation (Davidson, 1997, Tadu et al., 2014). The tramp crazy ant *P. longicornis* is an exploitative competitor and uses a foraging strategy with a recruitments occurring at a short-range of distance (Kenne et al., 2005). The numerical dominance of *P. longicornis* at baits is thought to be principally linked to its speed (Kenne et al., 2005). *Tetramorium* sp. and *Axinidris* sp. were numerically dominant less frequently than the other dominant taxa. However, when present at baits, *Axinidris* sp. displayed a high abundance score resulting in the control of a moderate proportion of baits.

We hypothesized that the vegetation structure determines which species numerically dominates ground-dwelling ant community at local (subplot) scale. We indeed found that the general trend of numerical dominance can be altered by the density of plants in the intermediate and high strata. The probability of being numerically dominant for ground-dwelling ants like *Pheidole* spp., *Monomorium* spp., and *Tetramorium sp.* decreased as the density of the intermediate and high strata increased, while the probability of being dominant for the mostly arboreal taxon *Camponotus* spp. and the tramp species *P. longicornis* increased with the density of plants in the intermediate stratum. A high density of high strata plants also increased the abundance of these taxa, but as the density of plants with leaves in the high stratum increased, the dominance of the strictly arboreal ant *Axinidris sp.* increased. We found no effect of the plant density in low stratum on the dominance of ants. Stevens et al. (2002) also found no effect of ground cover on the dominance of the Dolichoderinae ant *Iridomyrmex* in citrus groves. Together, these results suggest that plant density in the low stratum does not directly modify habitats for the functional groups to which the six studied taxa belong (Andersen, 1995). However, the low stratum may have influenced the functional group of cryptic ants (e.g., hypogaeic and litter-dwelling ants), as demonstrated by Bestelmeyer and Wiens (1996); that possibility should be investigated in future research.

According to Ribas et al. (2003), low and high woody plants densities may influence ant communities through three processes: (i) resources increase with woody plant density, and an increase in resources would enhance ant species diversity; (ii) habitat conditions are altered by the density of woody plants, and habitat conditions would affect which ants are numerically dominant; and (iii) the variation in woody plant densities may lead to species-area patterns. Our results on dominance hierarchies are in agreement with the second and third processes. Indeed, the effects of strata densities are consistent with the preferred ecological niches of the six studied ant taxa. For instance, ground-dwelling taxa were, in our study, negatively related to the density of arboreal habitats (e.g., intermediate and high strata). This agrees Lassau and Hochuli (2004) who found that the abundance of species that only nest on ground was negatively related to the density of tree cover. The abundance of *Camponotus* spp., which may forage both on the ground and in the arboreal stratum, was positively related to the density of high strata plants, which correspond to arboreal nesting or foraging habitats, except in the extreme densities of the high stratum, which coincided with the numerical dominance of *Axinidris sp.* The members of the latter genera nest strictly in trees and are primarily arboreal foragers but may occasionally forage in ground litter (Snelling, 2007) . We observed individuals of *Axinidris sp.* at baits only in the dry season, which is consistent with the view that arboreal ant species forage at ground-level during the dry season, when resources in trees are relatively scarce (Delabie et al., 2000). *Paratrechina longicornis*, known as the crazy ant, is a native of West Africa and prefers moist habitats for reproduction (Kenne et al., 2005). The nests of this tramp species are often small and ephemeral and occur in a wide range of habitats (e.g., plant cavities, live or dead plants, leaf litter). An increase in the density of plants with leaves in the intermediate and high strata may enhance the local hygrometry and therefore increase the nesting sites available for *P. longicornis*. However, *P. longicornis* is a weak competitor against common ground-dwelling ant species (including *Camponotus* spp*.)* in its native range (Kenne et al., 2005). We hypothesize that, as the density of plants with leaves in the high stratum increases in a plantain field, the availability of foraging and nesting sites increases, and better competitors like *Camponotus* spp. and *Axinidris sp.* dominate the area (Vasconcelos et al., 2008) and decrease the positive effect of the intermediate stratum density on *P. longicornis*.

We found no relationship between the numerical dominance of each ant taxon with the crop diversity. One explanation may be that the studied taxon were omnivores that feed in multiple trophic level (consumers of plant resources, hemipteran honeydew, herbivores, predatory arthropods or even scavengers), and may be not affected by the identity of plants that constitute only a part of their diet. One other explanation may be that the presence and abundance of species is linked to nesting habits. For instance, most *Camponotus* spp. forage both arboreally and on the ground but have specialized nesting habits in that they generally start colonies in living or dead trunks, such as banana pseudostems. Davidson (1997) argued that this kind of ant species locates its nest on preferred resource plants. Consequently, plant diversity would not modify their nesting or foraging habits.

Ants have also been increasingly recognized as important predators in tropical and subtropical agricultural systems (Way and Khoo, 1992, Perfecto and Castineiras, 1998, Offenberg, 2015). Ants have complex and often strong effects on lower trophic levels (Philpott et al., 2008) and may be useful in pest management (Perfecto, 1991). In plantain and banana agrosystems, the banana weevil *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae) is the most important pest (Gold et al., 2001). Using metabarcoding analysis and predation tests, Mollot et al. (2014) recently showed that *C. sordidus* is preyed on by the arboreal ant *Camponotus sexguttatus* F. (Hymenoptera: Formicidae) and the ground-dwelling ant *Solenopisis geminata*. In the current study, we have shown that *Camponotus* spp. were favoured by the intermediate and high strata. *Pheidole* spp. has been suggested to be a potential natural enemy of *C. sordidus* in Uganda (Abera-Kalibata et al., 2007, Abera-Kalibata et al., 2008), and *Pheidole megacephala* and *Tetramorium guinensee* (Bernard) (Hymenoptera: Formicidae) are used as biological control agents of *C. sordidus* in Cuba (Castineiras and Ponce, 1991, Perfecto and Castineiras, 1998). Our results indicate that the manipulation of the densities of crops with leaves in the intermediate and high strata may help maintain the coexistence of ant species by providing different habitat patches. Further research in such agrosystems should be performed to assess if the effect of vegetation structure on ant abundance could result in efficient pest regulation.

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Table 1(on next page)

Occurrence of dominant, subdominant, and subordinate ants at baits.

Genus/species	Baits recorded (%)		Baits controlled (%)		Mean abundance score	
	Rainy season	Dry season	Rainy season	Dry season	Rainy season	Dry season
Dominant						
Pheidole	36.8	43.6	25.54	37.16	3.35	3.76
Subdominant						
Axinidris sp.	0	10.4	-	13.46	-	4.19
Subordinate						
P. longicornis	32.6	36.8	10.43	9.24	2.83	2.75
Tetramorium sp.	11.2	13.4	7.14	19.4	2.41	3.16
Monomorium	37.2	34.8	9.14	6.32	2.63	2.33
Camponotus	41.0	40.2	6.83	8.46	2.64	2.46

Table 2(on next page)

Cultivated plant species in each stratum of diversified plantain-based agroecosystems.

Stratum refers to the location of the plant canopy relative to the soil surface.

Stratum	Cultivated plant species
Low	*Arachis hypogaea* L. (groundnut), *Xanthosoma sagittifolium* (Schott) (macabo), *Colocasia esculenta* L. (taro), *Dioscorea* spp. (yam), *Capsicum anuum* L. (hot pepper), *Solanum macrocarpon* L. (garden egg), *Corchorus* spp. (crin-crin), *Ananas comosus* L. (pineapple), *Amaranthus* spp., *Solanum lycopersicum* L. (tomato), *Abelmoschus esculentus* (Medik) (gombo), *Vigna unguiculata* L. (cowpea), *Ipomoea batatas* L. (sweet potato), *Zea mays* L. (maize)
Intermediate	*Carica papaya* L. (papaya), *Manihot esculenta* (Crantz) (cassava), *Vernonia* spp., *Gnetum africanum* (eru), *Triumphetta pentadra* (Rich.)
High	*Elais guineensis* (Jacq.) (oil palm), *Coffea Arabica* L. (coffee), *Theobroma cacao* L. (cocoa), *Cola acuminata* (Schotte & Endl.) (cola), *Dacryodes edulis* Lam (safou), *Persea americana* (Mill.) (avocado), *Psidium guajava* L. (guava), *Mangifera indica* L. (mango)
Musa	*Musa* AAA (banana), *Musa* AAB (plantain)

Table 3(on next page)

Likelihood ratio tests for the strata multinomial model.

Stratum refers to the location of the plant canopy relative to the soil surface. Intermediate, high, and low strata indicate a high density of plants with canopies at intermediate, high, and low strata, respectively.

Variable	Δ d.f.	Chi^2	p-value
Intercepts	5	333.29	**< 0.0001**
Plant diversity	5	7.68	0.174
Intermediate stratum	5	33.14	**< 0.0001**
High stratum	5	18.85	**0.002**
Musa stratum	5	10.00	0.075
Low stratum	5	9.96	0.076

Figure 1

Frequencies of numerical dominance of subplots for each ant taxon in the rainy and dry seasons.

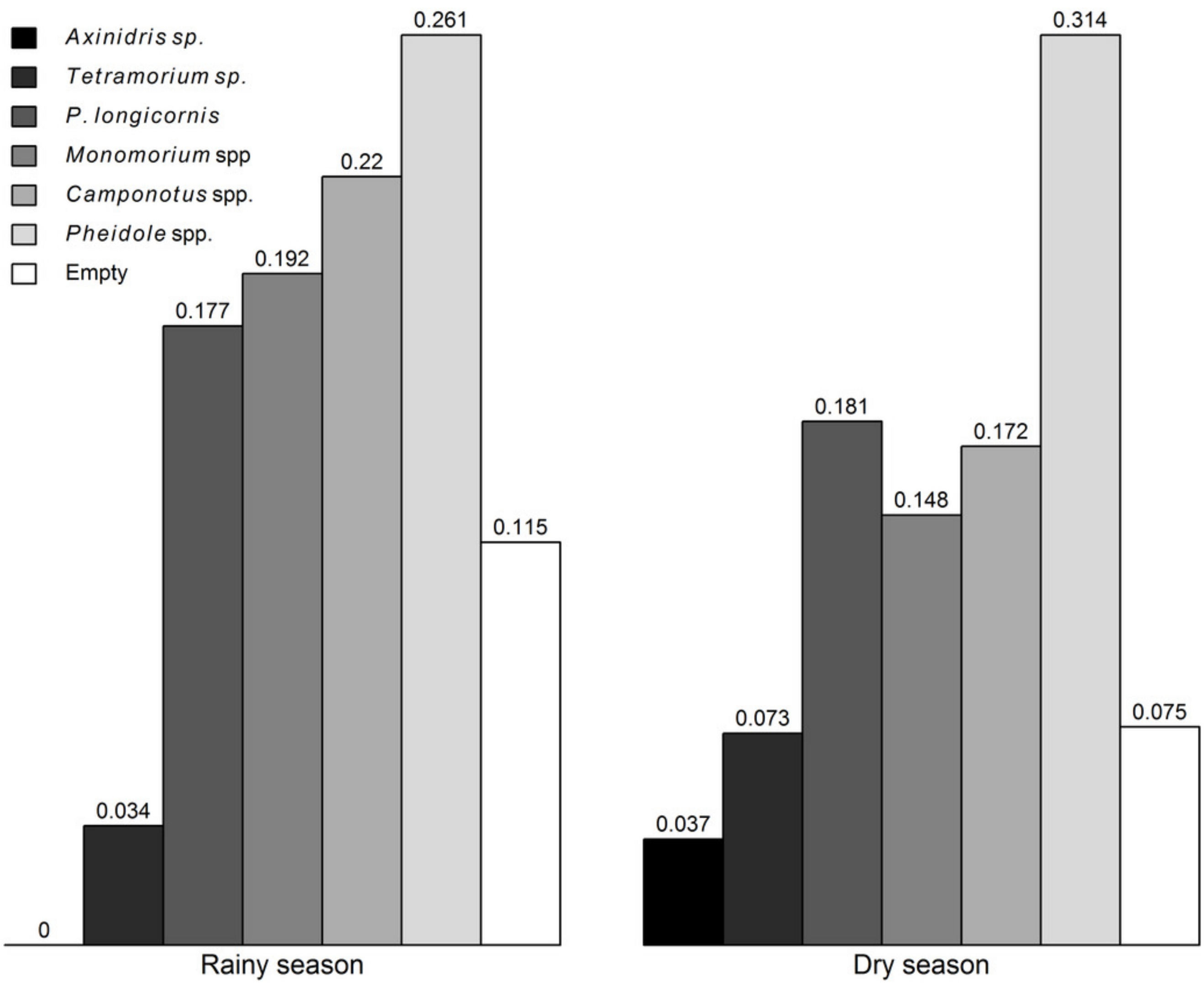

Figure 2

Predicted probability of dominance for each ant taxon.

Grey curves: response to plant density of intermediate stratum; Black curves: response to plant density of high stratum.