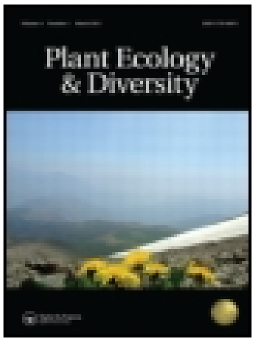

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ARTICLE

Giant stem rosettes have strong facilitation effects on alpine plant communities in the tropical Andes

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ABSTRACT
Background: Giant rosettes constitute one of the most distinctive growth-forms in tropical alpine ecosystems. However, their interactions with other plant species remain unexplored in high Andean páramos.
Aims: Quantify the effect of a dominant rosette (*Coespeletia timotensis*) on soil and microclimatic conditions and relate the impacts to plant community structure.
Methods: We analysed topsoil temperatures, soil organic matter (SOM) and plant species cover in areas adjacent to *C. timotensis* and paired areas outside, at three sites (4250–4360 m a.s.l.) in La Culata National Park, Venezuela. Species richness, total vegetation cover and percent cover of each species near and away from the rosettes were compared.
Results: Topsoil temperature amplitudes were lower and SOM greater near *C. timotensis* stems, compared to areas away from them. *C. timotensis* had a consistent positive effect on species richness, vegetation cover and the cover of many abundant species (including cushions and herbs).
Conclusions: The facilitation effects of *C. timotensis* on abiotic conditions and community structure indicate they play a key role as nurse plants, pointing to giant rosettes as foundation species for the maintenance of plant diversity in the alpine tropics.

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Diversity; ecosystem engineers; keystone species; nurse-plants; plant–plant interactions; relative interaction index; soil organic matter; temperature

Introduction

Positive plant–plant interactions (facilitation) are increasingly recognised as important structuring factors of community assembly and diversity (Bruno et al. 2003; Lortie et al. 2004; Callaway 2007). A major contribution to our understanding of the role played by facilitation in community organisation, has come from research on plants that modify microhabitat in their neighbourhood, ameliorate stress or generate resource islands ('biogenic ecosystem engineers' *sensu* Jones et al. 1997). These abiotic changes owing to so-called nurse-plant effects can, in turn, improve the establishment, growth and reproduction of beneficiary species, and increase plant diversity at local and/or community scales (Callaway 2007; Cavieres and Badano 2009; Filazzola and Lortie 2014).

Most studies on nurse-plant effects have involved shrubs in xeric environments and cushions in extra-tropical alpine ecosystems, where cushions are the main growth-form with the ability to ameliorate abiotic conditions and influence species abundance and diversity (Reid et al. 2010; Filazzola and Lortie 2014; Cavieres et al. 2016). However, tropical alpine ecosystems (TAE) are characterised by a diverse array of plant growth-forms of large size and longevity, which have the potential to act as nurse-plants or ecosystem engineers, including sclerophyllous shrubs, cushion plants, tussock grasses and giant stem rosettes (Hedberg and Hedberg 1979; Ramsay and Oxley 1997; Anthelme and Dangles 2012; Cáceres et al. 2015). The contrasting architectures of the different growth-forms characteristic of TAE could result in differences in their effects on above-ground vs. below-ground abiotic factors, and consequently, in complementary effects on community organisation (Crooks 2002; Filazzola and Lortie 2014; Sklenář et al. 2016). Moreover, given the outstanding species and functional diversity of TAE in the Andes, species-specific and growth-form specific nurse-plant interactions can be important, which could in turn play a key role in promoting species interdependence and diversity in tropical alpine communities (see Malatesta et al. 2016; Anthelme et al. 2017; Hupp et al. 2017).

Studies addressing the community effects of nurse plants in TAEs centre on the role of cushion and shrub growth-forms in modifying species abundance patterns and increasing local plant

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Supplementary material for this article can be accessed here.

cover and diversity (Sklenář, 2009; Farji-Brener et al. 2009; Anthelme et al. 2012, 2017; Cáceres et al. 2015; Hupp et al. 2017). Ramírez et al. (2015) and Schweiger et al. (2015) have also shown that sclerophyllous shrubs can improve the water balance of associated species, while Malatesta et al. (2016) reported successional interaction cascades involving pioneer cushions, shrubs and tussock grasses in the Peruvian dry puna.

However, plant–plant interactions involving giant stem rosettes and their effects on community organisation remain largely unexplored. This constitutes a major gap in our understanding of the role of plant–plant interactions in tropical mountains, as giant rosettes constitute one of the most distinctive and abundant growth-forms, dominating many high alpine landscapes across the northern Andes, East Africa, New Guinea and Hawaii (Hedberg and Hedberg 1979; Robichaux et al., 1990; Monasterio and Sarmiento 1991; Smith and Young 1987; Cuatrecasas 2013). The independent development of strong morphological and adaptive similarities of giant rosettes in different mountain systems in the tropics, e.g. in the *Dendrosenecio, Senecio* and *Lobelia* species of East Africa and species of the *Espeletia* complex in the northern Andes, constitutes a remarkable example of convergent evolution in alpine systems (Hedberg and Hedberg 1979; Monasterio and Sarmiento 1991). Moreover, the diversification and speciation process during the Quaternary of the *Espeletia* complex in the northern Andes (locally known as páramos), constitutes one of the world´s fastest plant adaptive radiations recorded (Madriñán et al. 2013; Diazgranados and Barber 2017; Pouchon et al. 2018).

Plant communities that develop in the paramos and other tropical alpine areas above 4000 m face a unique combination of environmental determinants that limit productivity. These include high incident radiation, large daily temperature amplitudes (≥30°C) far exceeding annual variations (≤3° C), and frequent night-time freezing. These conditions are linked with relatively low vegetation cover, low soil organic matter (SOM) and nutrient availability, and daily freeze-thaw soil cycles that result in limitations for plant water uptake, high superficial soil instability and active periglacial processes, including soil frost-creep (Schubert 1975; Monasterio 1986; Pérez 1987; Smith and Young 1987).

Giant rosettes exhibit a complex set of morphological and physiological adaptive strategies that have allowed them to successfully establish and become dominant under the harsh conditions of the cold tropics (see Hedberg and Hedberg 1979; Monasterio 1986; Smith and Young 1987; Monasterio and Sarmiento 1991; Pérez 1992; Rada 2016). Some of these adaptations are also likely to be important in influencing their potential role as nurse plants, including: (a) a large adult size and longevity prolonging their influence on local habitat conditions (e.g. 3-m-tall rosettes in the páramo can exceed 200 years of age); (b) a parabolic leaf arrangement increasing their ability to intercept incident radiation and water, which can then flow to the base of the rosette; (c) a high allocation to above-ground biomass, which can exceed 95%, and low investment in roots, potentially decreasing their competitive effect on neighbouring plants; and (d) a high proportion of standing necromass (up to 70% of total dry mass) in the form of dead leaves that remain permanently attached to the stem, acting as an isolating tissue for water stored in a central pith and as a nutrient reservoir (fragments can break and fall at the base). This standing necromass slowly decomposes along the stem with the participation of a diverse community of micro-arthropods and fungi (Ancona et al. 2005; Garay 1981; Sturm 1990), allowing for the partial re-utilisation of nutrients and turning the rosette into a sort of vertical micro-ecosystem (Monasterio 1986; Monasterio and Sarmiento 1991; Pérez 1992).

Previous studies in the northern Andes, East Africa and Hawaii have documented the role of giant rosettes in modifying microhabitat conditions in their neighbourhood, with lower topsoil thermal variability and needle-ice soil heaving close to rosettes (Pérez 1989, 2001), as well as higher values of SOM, water and nutrients (Pérez 1992, 1995, 1996, 2001; Mizuno 1998; Walker and Powell 1999). Studies on the rhizosphere of *Espeletia* in the Andes have also demonstrated the presence of a diverse array of fungi (including phosphorus solubilisers) and profuse mycorrhizal root colonisation (Cepeda et al. 2005; Coba 2005; Garcés et al. 2005). Additionally, some studies have documented nurse-plant effects of adult giant rosettes on conspecific seedlings (Smith 1981; Pérez 2001). However, none of these studies has quantified the effects of these biogenic changes induced by giant rosettes on the abundance and diversity of other plant species in the community.

In this study, we quantified the effects of a dominant giant rosette species, *Coespeletia*

Figure 1. Panoramic view of *Coespeletia timotensis* giant rosettes at one of the páramo study sites, Piedras Blancas, Sierra de La Culata National Park, Venezuela. All rosettes correspond to diferent sized plants of the same species.

timotensis (Cuatrec.) Cuatrec. (Cuatrecasas 2013) on local abiotic conditions and plant communities in the high páramos in Venezuela (Figures 1 and 2). Based on the available evidence on the effects of giant rosettes on microhabitat conditions (i.e. temperature buffering, resource islands), we hypothesised that: (a) giant rosettes would buffer topsoil temperature variability in their neighbourhood, and this effect would differ between east- and west-facing sides of the rosettes (as afternoons tend to be more cloudy in the páramos); (b) giant rosettes would increase SOM in their neighbourhood, the effect being more pronounced downslope from them; and (c) these positive effects on microhabitat conditions would result in directional facilitation effects of giant rosettes on plant cover and diversity in their neighbourhood, and significantly affect species distribution patterns, increasing the abundance of many other dominant species in these communities. Evaluating these hypotheses should contribute to our knowledge of the role of giant rosettes on the assembly and diversity of tropical alpine plant communities, by studying for the first time their facilitation effects on other species.

Materials and methods

Study area

The study was conducted in the Piedras Blancas páramo in the north-eastern sector of La Culata National Park in the Venezuelan Andes (8°52′N, 70°56′W). We selected three similar replicate study sites on north-facing slopes 1–3 km in distance apart: Site 1 (4250 m, slope angle 20–25°), Site 2 (4330 m, slope angle 20–25°), and Site 3 (4360 m, slope angle 15–20°). At all sites, the upper vegetation stratum was dominated by *C. timotensis* and all were covered by slope deposits and colluvial material resulting from the erosion and fragmentation of cirque walls and horns influenced by periglacial gelifraction processes (Schubert 1975; Monasterio 1979).

The study sites were located within the subnival belt, locally known as high Andean páramo or superpáramo (≥4000 m), in the driest region of the Venezuelan high Andes, with 860 mm of annual precipitation (Pico El Aguila Weather Station, 4118 m). The dry season extends between December and March (accumulating only 8% of the annual rainfall). Precipitation occurs mostly as rain, although snowfall can occur, particularly during the wet season (Monasterio 1986; Pérez 1992). Because of the equatorial location, mean monthly temperatures vary less than 2–3°C, and the growing season extends all year. However, there are large daily temperature oscillations, which accentuate during the dry season, when air temperatures can reach 25°C during the day and drop at night below −5° C (Monasterio 1986; Azócar and Rada 2006). Approximately 325 daily freeze-thaw cycles may occur during the year (at 4200–4300 m), promoting needle-ice formation on the soil surface and frost-creep processes (Schubert 1975). The soils are Entisols and Inceptisols, shallow, acid with a sandy to sandy-loam texture and a low SOM and nutrient contents (Pérez 1995).

The plant communities in our study sites have been defined as an open rosette páramo (Monasterio 1980), with two distinctive vegetation strata. The upper stratum reaches 0.5–3.5 m in height and cover between 5% and 30%; this stratum is dominated by dispersed giant rosettes of *C. timotensis* and *C. spicata* (that becomes more abundant at lower elevations and on gentler slopes than *C. timotensis*). Disperse shrubs of *Hypericum laricifolium* are also common in some areas. The lower stratum is also very patchy, with plant cover varying between 2% and 40%. This stratum is mainly formed by cushions (e.g. *Azorella, Arenaria, Aciachne*), small grasses (e.g. *Agrostis, Festuca*), erect herbs or forbs (e.g. *Senecio, Castilleja, Oxylobus*), postrate herbs (e.g. *Geranium, Lachemilla*) and acaulescent rosettes (e.g. *Hypochaeris, Oenothera, Draba*). The exotic forb *Rumex acetosella* is also abundant in this area (Cáceres et al. 2015).

Study species

The focal species was the giant rosette *C. timotensis* (Asteraceae, Espeletiinae), which is endemic to northern páramos and only found in Venezuela. *C. timotensis* is the most widely distributed giant rosette in our study region, growing between 4000 and 4600 m and reaching the highest densities from 4200 to 4400 m on moderate to steep slopes of glacial cirques on poorly differentiated substrates (Estrada et al. 1991). Demographic studies have indicated that it grows ca. 15 mm year^{-1}, reaching up to 3.5 m in height with a lifespan of more than 200 years (Monasterio 1986). *C. timotensis* has a dense monopodial stem that ends in a crown of large, pubescent evergreen leaves around the apical meristem, while dead leaves remain attached to the stem forming a thick cylinder (10–30 cm) accounting for more than 75% of the standing phytomass. The superficial (≤25 cm) roots, which extend radially 100–180 cm from the stem, contain about 3.5% of total biomass. The species is polycarpic and it reproduces via wind-dispersed seeds (Monasterio 1986; Pérez 1992).

At each of the three study sites we estimated, using the line-intercept method (Greig-Smith 1983), the cover of *C. timotensis* rosettes along four 50-m transects placed parallel to the slope, separated by 10 m (for a total of 12 transects across the three sites). At each site, we counted the number of rosettes present within three 10 m × 10 m plots, each randomly positioned in the space between two of the four transects. Rosettes were divided into two size classes: small (0–50 cm in height) and large (≥50 cm). This was done to assess if the study sites were similar in terms of rosette abundances. At Site 1, the average (±SD) cover of *C. timotensis* was 8.2% (±2.3), with a rosette density of 1.4 large individuals m^{-2} and 4.0 small individuals m^{-2}. At Site 2, the giant rosette cover was 6.2% (±2.4) with 1.8 large individuals m^{-2} and 1.9 small individuals m^{-2}. Finally, at Site 3, rosettes covered 12.3% (±5.1) with 3.4 large individuals m^{-2} and 8.4 small individuals m^{-2}.

Effect of giant rosettes on soil temperature and organic matter

At each of the three sampling sites, we randomly selected one *C. timotensis* individual larger than 1 m in height (which could be more likely to be old enough to have significantly modified abiotic conditions in their neighbourhood). We used three Tidbit v2 temperature sensors buried 2 cm below the soil surface for each selected individual (for a total of nine sensors across the three sites). Two sensors were placed in soils under the direct influence of the rosette, 15 cm from the base, one each positioned to the east and west of the rosette (all sites were on north-oriented slopes, Figure 2). We selected these orientations because in tropical alpine sites the largest difference in incident radiation is expected in this direction; east-facing areas tend to receive more insolation because there is a lower probability of cloud cover in the mornings (Azócar and Rada 2006). The third sensor was placed at a random orientation 3 m away from the base of the rosette, in bare soil areas, away from the immediate influence of the rosette stem. Temperatures were recorded every 10 min for 39 days during the transition from the wet to the dry season, including both cloudy and clear-sky days (5 November to 13 December 2015). We calculated the average of each temperature measurement from the three replicate sensors established in each of the three sensor positions relative to the rosettes.

SOM was measured by obtaining soil cores between 5 and 10 cm below the soil surface around 10 randomly selected individuals larger than 1 m in each of our three study sites. Given that previous studies in the area have indicated that the most marked effect of giant rosettes on adjacent soil conditions occur downslope from them (Pérez 1995), we took individual samples 15–20 cm from the base of each rosette, one sample upslope (to the south of the rosette) and one sample downslope (to the north, Figure 2). Then, we took two samples away from them, one upslope and one downslope from a point placed 3 m away from the rosette in a random direction. Hence, 40 soil samples were collected at each site and 120 across the three sites. SOM content was determined using the weight difference between a sample of dry soil, and the remnants of the sample after heating to 400°C for 4 h (Davies 1974).

For the analysis of the SOM data, values close and far from the rosette were first averaged for each replicate *C. timotensis* individual, irrespective of the slope direction. Average values for all replicate individuals were then compared using a two-way Permutational Analysis of Variance (using the PERMANOVA+ for Primer 6.0 software, Anderson et al. 2008), defining the local sampling situation as a fixed factor with two levels (close vs. far from the rosette) and the sampling site as a random factor with three levels (our three study sites). Then, to determine if there was a directional effect of the rosette on SOM values, we carried out a two-way PERMANOVA defining the local sampling direction as a fixed factor with two levels (upslope vs. downslope from the rosette), and the sampling site as a random factor with three levels.

Vegetation sampling

At each study site, within a 100 m × 100 m area, we randomly selected 40 *C. timotensis* individuals (≥50 cm in height) to quantify their influence on vegetation structure. Next to the base of each individual rosette we established four semi-circular sampling plots, each of a 0.393 m^2 in area (with the 100 cm diameter lying next to the stem), in each cardinal orientation, with the north always pointing downslope (Figure 2). Within each sampling plot, we visually estimated the cover of all plant species present. For comparison away from rosettes, we randomly selected a point 3 m away from each rosette and distributed the four semi-circular plots around this random point (Figure 2), as we did within the influence of the rosettes (making sure no other large rosettes were located near these plots). This distance was chosen as previous studies by Pérez (1995) have indicated that roots and the area of influence of rosettes on SOM and

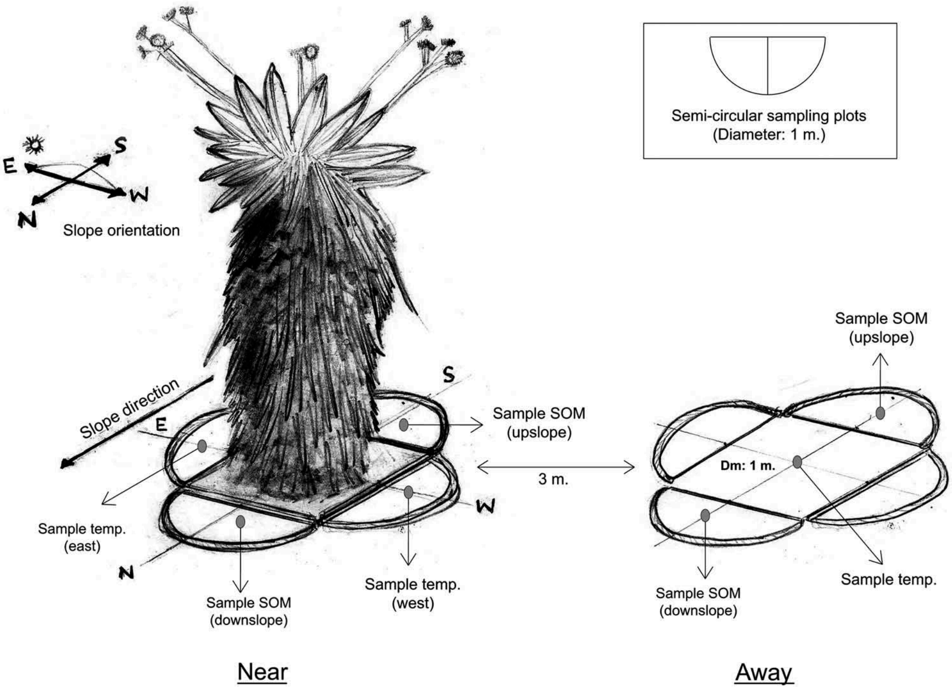

Figure 2. Schematic representation of the paired sampling design used to study the effect of giant rosettes on local abiotic conditions and plant community structure, using four semi-circular plots (100 cm in diameter) placed around each replicate individual of *Coespeletia timotensis* and 3 m away from them, Piedras Blancas, Sierra de La Culata National Park, Venezuela. The study slopes were always north-oriented. Hence, the semi-circular plots were always placed to the north (downslope), south (upslope), east and west of each replicate individual studied.

nutrients can reach between 1 and 2 m from the stem. Again, we determined the density and cover of all plant species present within each sampling plot. Hence, in each site, we sampled four semi-circular plots close to each of the 40 rosettes and four paired semi-circular far from each, for a total of 960 plots across the three sites. For taxonomic nomenclature we followed Briceño and Morillo (2002) and the Plant List (www.theplantlist.org).

Analysis of vegetation patterns

To quantify the overall effects of giant rosettes on local community structure, we first averaged the values for the cover of each species present within the four semi-circular plots placed in each cardinal direction around each *C. timotensis* individual. The same was done for the four replicate plots placed away of each individual. From this integrated data we then calculated the total vascular plant cover close to and away from each individual, by summing the cover off all species. Then, average total cover and average local richness were calculated for each situation (inside vs. outside the influence of the giant rosettes) and compared using a two-way PERMANOVA. Sample location was used as a fixed factor with two levels (close vs. away from the rosette) and the sampling sites as a random factor with three levels.

Rank-abundance diagrams were generated based on the average cover of each species, comparing close vs. away across the three sites. Then, to establish the local relationship of each plant species with *C. timotensis* we used the mean relative interaction index (RII; Armas et al. 2004) to compare the cover of each species close to the rosette with that away from them. RII was computed as $RII = C_{\text{rosette}} - C_{\text{open}}/C_{\text{rosette}} + C_{\text{open}}$ where C represents the cover of each species for each pair of samples. We then calculated means and 95% confidence intervals for the RII values across all 120 replicate pairs (40 per site), taking all sites together. RII values range from 1 to −1, where significant positive values (i.e. the 95% confidence interval does not include zero) suggest a positive effect of the giant rosette and significant negative values suggest inhibitory effects. We only calculated RII's for species that were present at least around two replicate individuals.

To obtain an integrated view of the species assemblages in microhabitats both close and away from the rosette, we constructed Bray–Curtis community dissimilarity matrices based on the square-root-transformed species cover data for each of the 40 replicate *C. timotensis* individuals in each site. The transformation decreased the weight of dominant species in the calculations. These matrices were subjected to principal coordinates analysis (PCoA). Average Bray–Curtis dissimilarities were compared using two-way PERMANOVA (using Primer 6.0 and PERMANOVA+ for Primer, Clarke and Gorley 2006; Anderson et al. 2008), using the sampling location as a fixed factor and the study sites as a random factor. To establish if giant rosettes affected total species richness near and away from rosettes we built Mao Tau rarefaction curves (1000 randomisations) using the 40 replicate samples in each site and estimated the total species richness at saturation using a Bootstrap procedure with Primer 6.0.

Finally, we analysed if there was a directional effect of the giant rosettes on local community attributes, and if these effects were consistent across study sites. For this, we calculated the total plant cover and species richness of the semi-circular plots oriented to the north, south, east and west of each *C. timotensis* individual sampled. These values were compared using two-way PERMANOVA, defining the sampling direction as a fixed factor with four levels (the four cardinal directions) and the sampling site as a random factor.

Results

Effects of C. timotensis *on soil temperature and organic matter*

We found clear differences in average topsoil temperatures between cloudy and clear days and between sensors close to *C. timotensis* (in west and east orientations) and 3 m away from them (Figure 3). Close to rosettes daily thermal variability was lower compared to the soil temperature variability away from the rosettes; the dampening effect was stronger east of the rosette and during clear days. This pattern was consistent across the three study sites. The dampening effect was mainly associated with a reduction in maximum temperatures near *C. timotensis*, with an observed average maximum of 21.7°C in open soils vs. 16.8°C and 10.8°C to the west and east of the rosette respectively (during the 39 days of measurements). For minimum temperatures, differences were less pronounced, with an average of −0.2°C outside vs. 0.7°C to the west and 1.2°C to the east of the rosette.

When average SOM was compared between samples collected near the rosette and away from them across the three sites, we found a significant

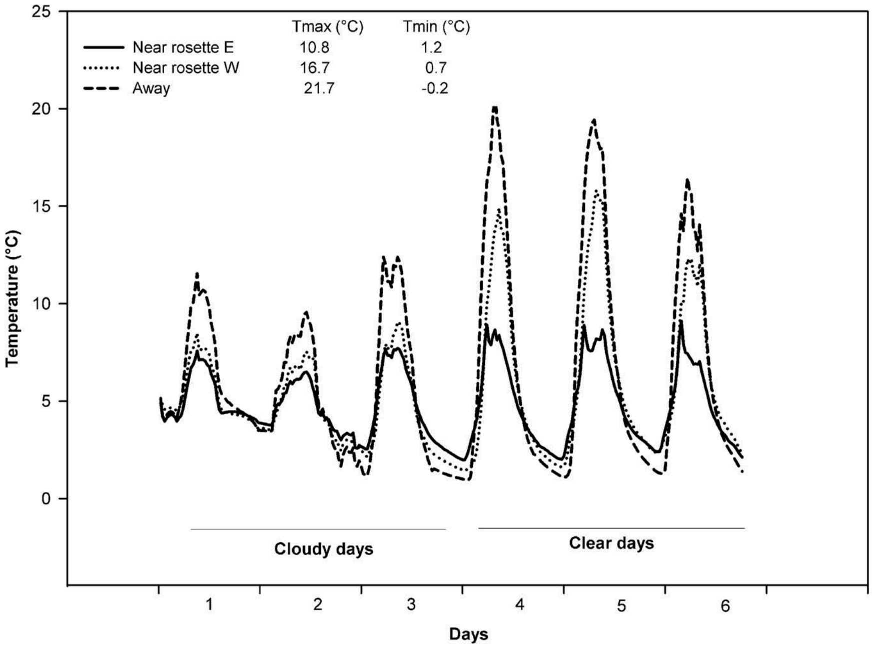

Figure 3. Average topsoil temperatures (−2 cm) near the base of *Coespeletia timotensis* giant rosettes (to the east and west of the base) and in areas outside their direct influence (3 m away from the base) at three páramo study sites, Piedras Blancas, Sierra de La Culata National Park, Venezuela. The plotted lines correspond to average temperature values recorded every hour during 6 representative days with both cloudy and clear skies; the average daily maximum and minimum values presented next to the legend correspond to temperatures registered during the whole study period (5 November to 13 December 2015).

Table 1. Average soil organic matter (5–10 cm) sampled next to giant rosettes of *Coespeletia timtensis* and in areas 2–3 m away from the stem in three sampling sites in the Piedras Blancas Páramo, Venezuela. The overall average from all replicate samples in open ground and next to rosettes were compared (n = 20); average values of samples obtained upslope (to the north) and downslope (to the south) from the rosettes (n = 10). Different letters indicate significant differences between average values (pair-wise *t*-tests).

Sample position	Site 1	Site 2	Site 3
Away from rosettes	1.17 ± 0.12a	1.84 ± 0.14a	1.93 ± 0.22
Rosette base	2.23 ± 0.21b	3.82 ± 0.57b	2.45 ± 0.25
Downslope (N)	2.14 ± 0.17	3.19 ± 0.60	2.54 ± 0.41
Upslope (S)	2.31 ± 0.40	3.94 ± 0.60	2.37 ± 0.30

interaction between the two factors (sampling distance from rosette / site, P = 0.03), indicating that the local effect of the rosettes on SOM differed among sites (Table 1). Average SOM values were significantly higher next to rosettes than away from them at Sites 1 and 2 (pair-wise *t*-tests, P < 0.01 and P < 0.001), but not at Site 3 (P = 0.11). There was no significant difference between samples downslope (S) vs. upslope (N) (P = 0.57), this being consistent across sites (no significant interaction between both factors, P = 0.26).

Effects of C. timotensis *on species richness and vegetation cover*

We found higher average local species richness and total plant cover when comparing samples close vs. far from the rosettes across the three study sites (Figure 4). For both variables, the two-way PERMANOVAs indicated a significant difference (P < 0.05 for richness and P < 0.05 for cover) between near the rosette and away from them, with no significant site effect and no significant interaction between the factors. Higher average local richness was associated with a higher aggregated total number of species observed within all sampling units next to the rosettes compared to away samples at each of the three study sites, with six to nine more species recorded in the sampling units near *C. timotensis*. This was confirmed by the bootstrap estimation of species richness at saturation (Table 2).

There was a significant effect of sample orientation (Figures S1 and S2) with respect to the rosettes of *C. timotensis* on local species richness (P < 0.05), but no effect on plant cover. In the case of local average richness, the pair-wise *t*-tests indicated that sampling units

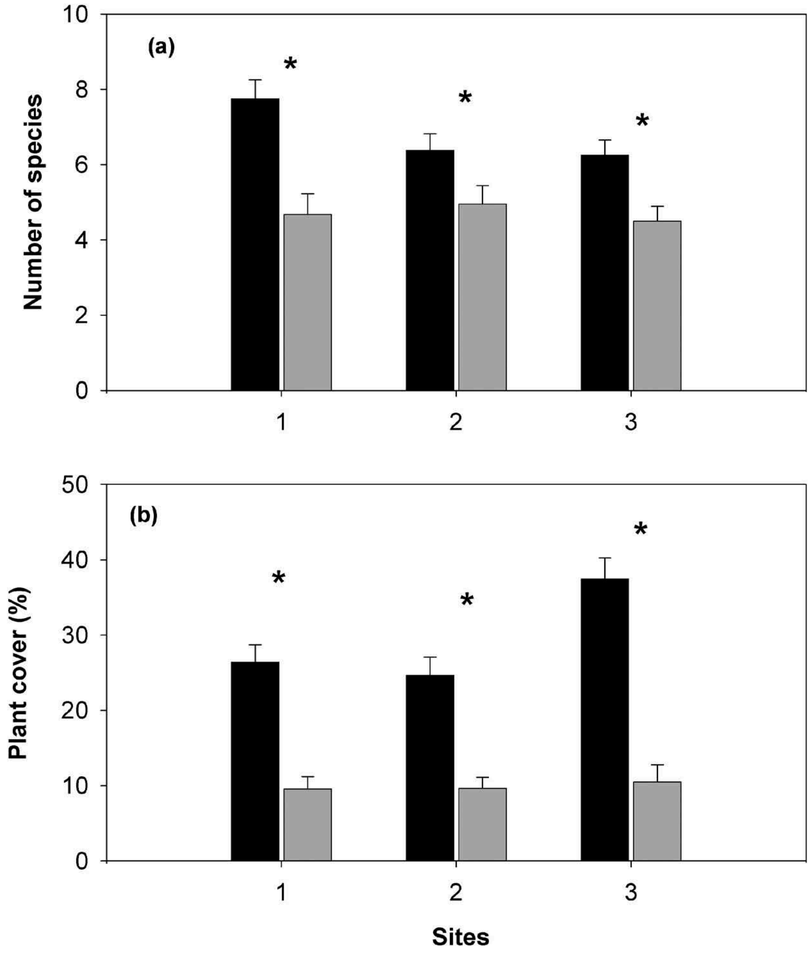

Figure 4. Average plant species richness (a) and plant cover (b) recorded in micro-plots placed inside (black bars) and outside (gray bars) the direct influence of *Coespeletia timotensis* giant rosettes (n = 40) at three study sites in the Piedras Blancas Páramo, Venezuela. Asterisks indicate significant differences between sampling plots inside vs. outside the local influence of the rosettes across the three sites (two-way PERMANOVA, $\alpha = 0.05$).

Table 2. Total observed species richness and estimated maximum richness (boostrap) near the stems of *Coepeletia timotensis* giant rosettes vs. areas away from the stems in three study sites in the Piedras Blancas Páramo, Venezuela.

	Observed richness		Bootstrap	
Site	Rosette base	Away	Rosette base	Away
1	42	33	45.8	37.9
2	38	32	42.6	35.6
3	32	26	35.9	29.4

to the north of the rosettes (downslope) had a significantly higher number of species than sampling units in other orientations ($P \leq 0.05$) in the three study sites (Figure S1).

Effects of C. timotensis *on species abundance patterns*

The integrated rank-abundance diagram for the three study sites (Figure 5) indicated clear differences in local community structure, with a higher cover of many species near *C. timotensis*, especially the most abundant ones. Among these abundant species, the forbs *Castilleja fissifolia, Senecio wedglacialis, Pentacalia imbricatifolia, Oxylobus glanduliferus* and *Mona meridensis*, the cushion plants *Azorella julianii* and *Arenaria* sp. and the grass *Agrostis tolucensis* showed a positive association with *C. timotensis*, with RII's significantly >0. In contrast, only one species, the grass *Agrostis breviculmis*, showed a clear negative association with the rosette, with an RII significantly below zero (see Table S1 for the complete species list).

The PCoA of species cover values in samples near to and away from *C. timotensis* stems (Figure 6) indicated the same general patterns observed in the rank-abundance diagrams. There was a clear separation between sampling units close to or away along the first and second principal coordinates (explaining 15.6% and 11.1% of the total variation), with some degree of overlap.

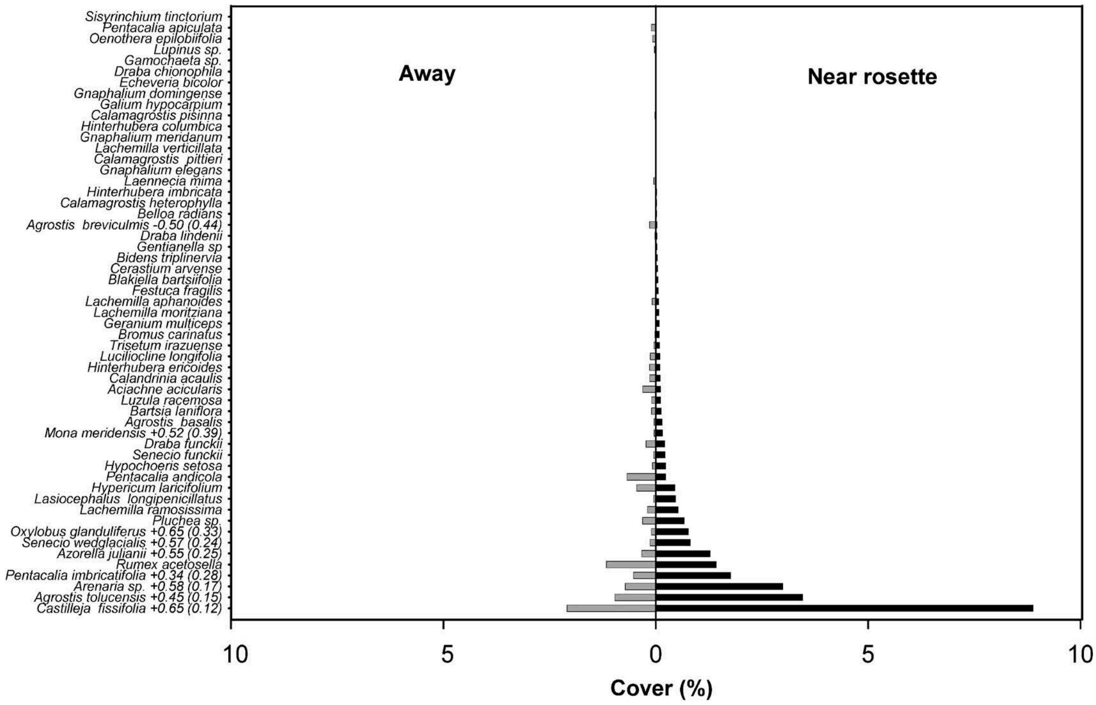

Figure 5. Rank-abundance diagram of the average cover of vascular plants recorded in micro-plots placed inside and outside the direct influence of *Coespeletia timotensis* giant rosettes (n = 120) across three similar study sites in the Piedras Blancas Páramo, Venezuela. Species are ordered according to their cover near the rosettes. The relative interaction index (RII ± 95% confidence interval) is presented next to the name of those species that showed a statistically significant positive or negative association with *C. timotensis* (i.e. the 95% confidence interval did not include zero).

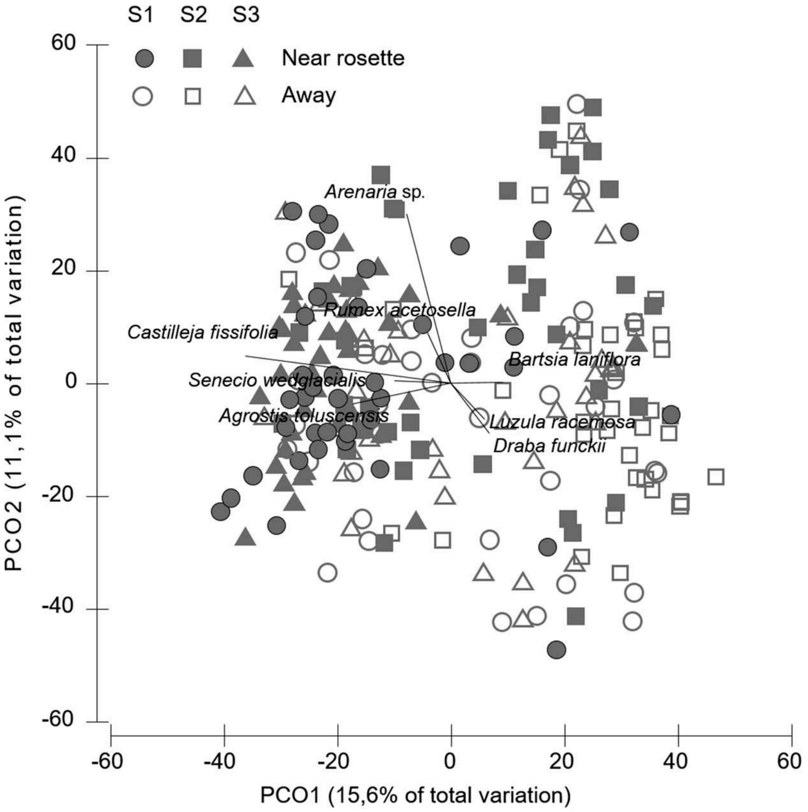

Figure 6. Principal coordinates analysis (PCoA) based on a Bray–Curtis similarity matrix of the cover of vascular plants in micro-plots placed inside (grey symbols) and outside (white symbols) the direct influence of *Coespeletia timotensis* giant rosettes (n = 40) in three study sites (s1, s2, s3) in the Piedras Blancas Páramo, Venezuela. The vectors correspond to the Spearman Rank correlation ($R_s \geq 0.15$) of species cover with the plot scores on the first two principal coordinates.

Samples close to the giant rosette where associated with a higher cover of *C. fissifolia, S. wedglacialis* and *A. tolucensis* along the first axis and with higher cover of *Arenaria* spp. and *Rumex acetosella* (an exotic species) along the second axis. The species with high cover away from the rosettes included *Bartsia laniflora, Luzula racemosa* and *Draba funckii*. There was a significant effect of the local sampling position (close vs. far from the rosettes´ influence, two-way PERMANOVA, $P < 0.001$), indicating a consistent significant effect of *C. timotensis* on local community structure. We also found a significant effect of the study site ($P < 0.001$), pointing to differences in community structure owing to spatial heterogeneity at the landscape scale.

Discussion

Effects of giant rosettes on microhabitat conditions

Wide temperature amplitudes, with freezing nocturnal minima and high diurnal maxima (associated with high solar radiation inputs), can have important consequences for the thermal balance and water economy of tropical alpine plants, especially during the dry season (Rada et al. 2018). Our results indicate that the presence of *C. timotensis* is associated with a decrease in topsoil thermal variability compared to open soils, particularly by reducing daily temperature maxima (as much as 10.9 K). The reduction in topsoil maximum temperatures (and thus in potential evapotranspiration) could be indicative of lower radiation loads during clear days in their neighbourhood, which could have positive effects on superficial soil water availability (see Pérez 1992) and on the leaf energy and water balance of associated species, particularly those that grow close to the ground (a hypothesis that remains to be tested). Interestingly, rosettes had a stronger moderating effect on temperature maxima on their east-facing side than on their west side. This could have been the result of a lag effect in soil warming during the day, as the soils towards the west of the rosettes reached maximum temperatures after midday, when the soils to the east were possibly already being shaded by the rosettes.

The presence of *C. timotensis* also corresponded to a less pronounced increase in soil temperature minima (ca. 1 K). Although this warming effect was small, Pérez (1989) has reported in the same study area a sharper increase in air temperature minima 10 cm above the soil surface close to *C. timontensis* stems, where it reached −2°C compared to −9°C in open areas. Hence, the positive effect of giant rosettes on minimum temperatures close to the ground could in turn reduce the frequency of soil water freezing and the formation of needle-ice during the night and early morning, thereby reducing soil instability (Pérez 1989), as well as frost damage and water stress for associated plants. Even so, using a higher number of replicate sensors, monitoring both air and topsoil temperatures (as well as leaf temperatures of associated plants) would be important to derive more definitive conclusions on the microclimatic effects of giant rosettes.

SOM showed 75% higher average values adjacent to giant rosettes compared to those away from the rosettes. Similar increases in SOM have been reported by Pérez (1995), ranging between 50% and 150% depending on local conditions. However, the actual SOM values found by us were consistently lower than those previously reported by Pérez (1992, 1995), probably due to differences in soil sampling depths (5–10 cm in our samples vs. 0–10 cm in previous studies). Interestingly, Pérez (1992, 1995, 1996) has reported a clear association between the increase in SOM near *C. timotensis* and a marked increase in soil water and nutrients in their neighbourhood (including soil bases, total N and P), pointing to giant rosettes as biogenic resource islands. Similar effects on soil water and nutrients have been reported for cushions both in tropical and extra-tropical sites along the Andes (Anthelme et al. 2012; Cavieres et al. 2006, 2008).

Contrary to our expectations, we did not find significant differences in SOM values in samples downslope from the rosettes compared to samples upslope. This may be attributed to the prevailing wind direction in our study area (northeast, Pérez 1995), which could have reduced SOM accumulation in areas north/downslope from the rosettes. This could be especially true given the moderate slopes studied (15°–25°), which could reduce the relative importance of slope vs. wind effects. In fact, Pérez (1995) showed that *C. timontensis* could modify SOM values not only through the incorporation of necromass to the soil, but also by reducing the influence of superficial soil erosion by winds; the effect of wind was more evident on shallow slopes, while SOM showed a stronger accumulation downslope from the rosettes in steeper sites.

Previous studies on nurse plants in our study area (Ramírez et al. 2015; Hupp et al. 2017) have also evaluated the effects of abundant cushions (*Azorella julianii* and *Arenaria musciformis*) and shrubs (*H. laricifolium*) on the microhabitat for associated plant communities. Cushions had very similar effects on topsoil temperatures than those reported here for giant rosettes, with a pronounced reduction of temperature maxima (12–8 K) and a less significant increase in temperature minima (ca. 1 K, see also Anthelme et al. 2011). Interestingly, the compact canopy of *H. laricifolium* shrubs had stronger buffering effects, with a reduction of 15 K in topsoil temperature maxima and a 5 K increase in the minima. Even so, shrubs seemed to induce a more moderate local increase in SOM under their direct influence (38%), followed by cushions (42–48%) and giant rosettes (75%).

Although these contrasting growth-forms all have positive effects on microhabitat conditions, they seem to modify below-ground vs. above-ground abiotic drivers to different degrees, which could result in complementary facilitation effects that need to be further studied. The compact crowns of shrubs seem to have particularly strong buffering effects on microclimatic conditions, sharply reducing incident radiation, increasing air humidity, and improving the water stratus of associated species (Cáceres et al. 2015; Ramírez et al. 2015). In turn, the positive effects of giant rosettes and cushions on SOM and soil resources (see also Pérez 1992, 1995; Anthelme et al. 2011; Cavieres et al. 2006, 2008) could be particularly important in driving their facilitative effects on associated species.

Effects of giant rosettes on plant community structure

We found higher average plant species richness and vegetation cover in the neighbourhood of *C. timotensis* compared to areas outside their immediate influence, plant cover being more than double near the base of the rosettes across the three study sites. Interestingly, the effect of giant rosettes on plant cover and local richness seems to be stronger and more consistent across sites than those previously reported for cushions and shrubs in the same study area (Cáceres et al. 2015; Hupp et al. 2017). When we explored if these effects had a directional component around the rosettes, we found no difference in the four cardinal orientations for vegetation cover, but average species richness was consistently higher downslope (north) of the rosettes across sites. This finding could be linked with the more positive effects of *C. timotensis* on soil nutrients downslope from them (nutrients predominantly flow downhill dissolved in water), as previously reported by Pérez (1995). However, since we did not find a significant increase in SOM downslope from rosettes, other factors could be involved, such as substrate stabilisation by *C. timotensis* stems.

At the community scale, both observed and estimated (bootstrap) species richness were consistently higher near giant rosettes than in areas outside of their immediate influence, with six to nine more species recorded near the rosettes at each site. However, the bootstrap estimates of species richness at saturation were slightly above the observed richness within our sampling plots. Hence, a higher number of replicate samples could be necessary to establish with certainty if there are species that are fully dependent for establishment and growth on the presence of *C. timotensis* (as has been shown by Cavieres and Badano 2009 for beneficiary species of cushions in alpine ecosystems of the central and southern Andes).

C. timotensis significantly modified local community structure, strongly altering local dominance hierarchies and species abundance patterns. This was true across our three study sites, even though they showed some differences in community composition and structure (Figure 6). RIIs indicated eight species with a significant positive association with *C. timotensis*, suggesting a net facilitation effect, including abundant forbs, cushions and grasses. Many of the same forb species have been reported to be positively associated with the common sclerophyllous shrub *H. laricifolium*, which was shown to have a positive effect on their water status in the same study region (Cáceres et al. 2015; Ramírez et al. 2015). In the case of *C. fissifolia*, this could be attributed to the known hemiparasitic character of species belonging to the genus *Castilleja* (Adler 2003).

The positive association between *C. timotensis* and the cushions is interesting, as cushions have been shown to act themselves as nurse plants in these páramos, increasing local plant cover and richness and the abundance of several species (Hupp et al. 2017). However, the beneficiary communities of *C. timotensis* and of the cushions differ, suggesting these systems exhibit growth-form specific and complementary facilitation effects, which could in turn increase beta diversity and promote species interdependence and coexistence (Callaway 1998, 2007). For example, while *Agrostis tolucensis* is positively associated with our focal giant rosette, its congeneric, *Agrostis breviculmis* is positively associated with both *Azorella* and *Arenaria* cushions, but not with *C. timotensis* (Hupp et al. 2017). In fact, *A. breviculmis* was the only species with a significant negative association with our focal rosette.

The positive association between giant rosettes and cushions offer support for the existence of positive interaction cascades between nurse plants in TAE, as recently suggested by a study in the Central Andes involving cushions, shrubs and tussock grasses (Malatesta et al. 2016). One possible strategy to further evaluate this hypothesis would be the analysis of plant–plant interaction networks between nurse plants of different sizes and growth-forms, and the other plant species growing in these functionally diverse communities (e.g. Losapio and Schöb 2017). In addition, *in situ* manipulative experiments (e.g. transplants) and comparison of the functional response of species associated with different nurse plants (Ramírez et al. 2015; Danet et al. 2018) could contribute to establishing a more mechanistic link between observed differences in microhabitat amelioration and species-specific patterns of spatial association. There is also a need to explore the generality of these positive interaction patterns between nurse plants and other plant species, replicating this type of studies across different regions.

Conclusions

The results presented here indicate that giant stem rosettes (*C. timotensis*) play an important role as nurse plants in the high tropical Andes, quantifying for the first time their strong positive effects on local plant species richness, vegetation cover and the abundance of many other plants in the community, including common forbs, cushions and grasses. These results point to giant rosettes as keystone or foundation species in TAE, not only in terms of their amelioration effects on the abiotic environment but also by virtue of their facilitation effects on many other abundant plant species.

The distribution of giant rosettes such as *C. timotensis* tends to be restricted to the highest elevations in the areas they occupy, so they could be particularly exposed to habitat losses induced by climate change (see Mavárez et al., 2018). They also seem to be the most sensitive growth-form to future changes in temperature and precipitation in the páramos (Rada et al. 2018). Given that our results suggest giant rosettes can play a key role as foundation species, their eventual local extinction could in turn produce negative effects for many other beneficiary species in these diverse tropical alpine communities (including secondary extinctions, something that could be tested experimentally). Moreover, the coexistence of different growth-forms which function as keystone species in TAE, including shrubs, cushions and giant rosettes, opens interesting research avenues to study how their interacting effects influence community assembly, and to further explore the extent to which their effects on biodiversity and ecosystem functioning are redundant or complementary (as the available evidence suggests).

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Disclosure statement

No potential conflict of interest was reported by the authors.

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