



# Impacts of climate, soil and biotic interactions on the interplay of the different facets of alpine plant diversity



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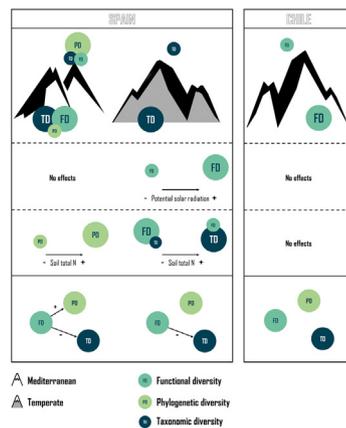
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## HIGHLIGHTS

- Links among ecological factors and alpine plant diversity facets are idiosyncratic.
- Elevation does not always negatively affect diversity facets in plant communities.
- Indirect effects of elevation can modify direct links between two diversity facets.
- FD is a cornerstone of community assembly, but it is not the panacea.

## GRAPHICAL ABSTRACT



## ARTICLE INFO

### Article history:

Received 27 May 2019

Received in revised form 16 August 2019

Accepted 16 August 2019

Available online 28 August 2019

Editor: Charlotte Poschenrieder

### Keywords:

Biotic and abiotic factors

Community assembly

Ecological gradients

Facets of alpine plant diversity

Structural equation models

Species interactions

## ABSTRACT

Disentangling the processes that drive plant community assembly is critical for understanding the patterns of plant diversity. We studied how different abiotic and biotic factors shape the interplay between the facets of alpine plant diversity, functional (FD), phylogenetic (PD) and taxonomic diversity (TD), in three different mountain ranges with contrasting evolutionary histories and climate conditions (Pyrenees and Mediterranean-type mountains in central Spain and Chilean Andes). We hypothesized that the causal links vary in strength and sign across regions. We used species inventories, functional trait data, and a phylogeny from 84 plant communities spread throughout three high-mountain alpine grasslands. Structural equation models were used to test our causal hypotheses on the relationships observed between the three diversity facets, and the abiotic (elevation, potential solar radiation and soil total nitrogen) and biotic factors (C-score). Despite our causal model presented a high variability in each mountain range, TD always decreased with increasing elevation (sum of direct and indirect effects). We also found some patterns suggesting that assembly processes could be climatically/biogeographically structured such as the negative relationship between FD and elevation found in Mediterranean mountains and the negative relationship between FD and TD found in both Spanish mountain ranges (independently of their different climates). A remarkable finding of this study is that ecological factors such as soil total nitrogen and elevation indirectly alter the relationships between the diversity facets. Our results suggest that

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diversity facets are simultaneously affected by different ecological and biogeographical/evolutionary processes, resulting in some general trends but also in parallel idiosyncratic patterns. Our findings highlight that although FD stand out by its explanatory power of community processes, TD and PD provide a complementary and necessary view that should not be disregarded in the attempt to globally explain community assembly processes.

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## 1. Introduction

Disentangling the underlying mechanisms driving the assembly of plant species in natural communities is critical for understanding the uneven distribution and the patterns of plant diversity (Diamond, 1975; Gotelli and McCabe, 2002; Keddy and Weiher, 1999). Among the main deterministic factors, abiotic conditions and plant-plant interactions play crucial roles in determining species co-occurrence and abundance distributions in plant communities. Traditionally, species richness and abundance distributions have been used to infer community assembly processes (Grytnes and Vetaas, 2002; Rosenzweig, 1995; Willig et al., 2003). However, this perspective unrealistically assumes that species are ecologically equivalent and evolutionary independent (Safi et al., 2011; Swenson, 2011). Therefore, during the last two decades, functional and phylogenetic perspectives have emerged for quantifying ecological and evolutionary processes on community assembly overcoming the inherent limitations of the so-called taxonomic approach.

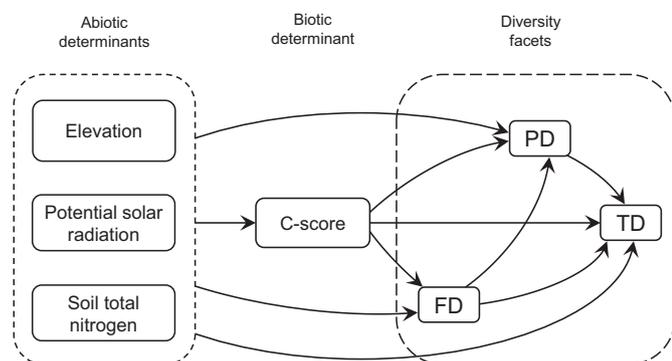
The functional perspective of community assembly (also called “trait-based ecology”) suggests that biotic and abiotic factors act as ecological filters allowing species to enter into the community on the basis of their functional trait values (Cornwell and Ackerly, 2009). This implies that only species with the appropriate set of morphological, physiological, and ecological traits will be able, at least in probabilistic terms, to enter into the natural assemblages and persist successfully (Shipley et al., 2016; Violle et al., 2007). This plant trait-based framework has led over the last decades to the need to incorporate functional information in the studies of community assembly, and indirectly, the explicit consideration of the phylogenetic structure of the assemblage. Phylogenetic approach is based on the premise that relevant functional traits have phylogenetic signal (i.e., closely related species are ecologically/functionally more similar). If so, the quantification of the phylogenetic relatedness among species would provide critical information regarding local-scale ecological assembly processes (Le Bagousse-Pinguet et al., 2017; Pavoine et al., 2011; Webb et al., 2002). This reductionist perspective is being currently changed since the phylogenetic structure substantially improves our understanding of the evolutionary processes that have shaped current patterns of biological diversity (Gerhold et al., 2015; Hughes and Eastwood, 2006). For instance, the phylogenetic structure may reflect the habitat age on the geological history with phylogenetic overdispersed patterns in more ancient habitats, at least at a relatively large scale (Lososová et al., 2015).

Diversity of a realized plant assemblage can be decomposed into three facets, functional (FD), phylogenetic (PD) and taxonomic diversity (TD), which reflect different ecological and evolutionary responses of communities to environmental determinants and historical events. Although they constitute independent axes of variation, there are causal relationships between them that need further exploration to better understand the mechanisms behind species coexistence (Swenson, 2011). For instance, when functional uniqueness predominates in species traits, a strong and positive correlation between FD and TD is expected (equally complementarity: Petchey and Gaston, 2002). This would mean that there is almost no functional redundancy among species, so each taxonomic label (i.e., species name) would correspond to a unique functional configuration. Consequently, emergence of positive correlations between these two diversities might reflect the importance of niche specialization as a mechanism of community assembly and diversity driver. In contrast, low levels of FD together with high levels of TD

might be a consequence of a strong environmental filtering (Keddy, 1992; Kraft and Ackerly, 2010) which would increase functional redundancy among species (Cadotte et al., 2011). On the other hand, the relationship between FD and PD could be structured according to the existence of a phylogenetic signal of the functional traits. That is, high FD values could lead to high PD values if phylogenetic conservatism prevails among the functional traits selected to estimate the FD (Webb et al., 2002). Although community ecologists have described some pairwise relationships between these diversity facets and their main structuring factors for inferring past and ongoing community assembly processes (Cadotte et al., 2013; Kraft and Ackerly, 2010; Swenson, 2011), to our knowledge, no previous studies have evaluated how abiotic conditions and plant-plant interactions influence the interplay between TD, FD and PD. Here, we propose a new theoretical picture in which FD plays a central role in the community assembly because individual plants entry in the realized assemblage through their functional architecture and, consequently, affecting the other diversity facets.

In this context, alpine plant communities are one of the most adequate models to disentangle the interplay between the diversity facets. Mountains show sharp and foreseeable environmental changes with elevation, a surrogate of climatic variation (Sanders and Rahbek, 2012). Recent studies suggest that shifts in elevation and other abiotic variables such as solar radiation have important consequences not only in TD but also in FD and PD. For instance, increasing elevation have been associated with environmental filtering constraining FD (de Bello et al., 2013; Read et al., 2014), PD (Jin et al., 2015; Xu et al., 2017) and TD (Cuesta et al., 2017; Rahbek, 1995), although other relationships have also been found (Le Bagousse-Pinguet et al., 2017; López-Angulo et al., 2018b). There are other critical abiotic factors acting at finer scales in high mountain environments such as soil total nitrogen, considered as the main limiting nutrient in alpine ecosystems (Sundqvist et al., 2014), and solar radiation (de Bello et al., 2013). In addition, biotic interactions, especially positive ones, are known to play a key role in the community assembly in high-mountains (Callaway et al., 2002; Cavieres et al., 2014) leaving also imprints not only in the functional structure (Pescador et al., 2015), but also in the taxonomic (López-Angulo et al., 2018a) and phylogenetic structures (López-Angulo et al., 2018b). However, to know whether or not the relationships between the diversity facets considering simultaneously the effects of multiple environmental factors vary across regions with contrasted climatic conditions and evolutionary histories remains largely unexplored.

Here, we aimed to evaluate the direct and indirect effects of key abiotic factors (elevation, soil total nitrogen, potential solar radiation) and biotic interactions on the interplay between TD, FD and PD in three contrasting mountain ranges. Specifically, we tested our causal framework and hypotheses underlying the relationships between these environmental factors and the three diversity facets (Fig. 1) using a context of pairwise comparisons between mountains differing in: 1) evolutionary and biogeographical history but with similar climate conditions (Mediterranean mountains from Spain and Chile), and 2) mountains with contrasted climatic conditions but a common evolutionary history (Mediterranean and temperate mountains in the Iberian Peninsula). More specifically, we hypothesize that: (a) some of the expected negative relationships between the three diversity facets and the elevation gradient (de Bello et al., 2013; Jin et al., 2015; Rahbek, 1995; Read et al., 2014; Xu et al., 2017), may be altered by some environmental factors related to local climate such as the typical summer drought of Mediterranean-type climates and exacerbation of stressful conditions



**Fig. 1.** Theoretical a priori conceptual causal model including the effects of abiotic (i.e., elevation, potential solar radiation and soil total nitrogen) and biotic determinants (i.e., C-score) on the three diversity facets (TD, FD and PD). Arrows represent direct causal relationships. Abbreviations: TD, taxonomic diversity; PD, phylogenetic diversity; FD, functional diversity; C-score, checkerboard score.

at low elevations (Giménez-Benavides et al., 2007; Mihoč et al., 2016); (b) FD plays a stronger role in community assembly than PD and TD, although these two facets provide unique and not concomitant insights into assembly processes; and (c) the relationships between PD and the environmental factors are maintained on the regions sharing biogeographical history as outcome of regional evolutionary processes.

## 2. Materials and methods

### 2.1. Study sites

We sampled three mountain ranges representing different climatic conditions and biogeographic/evolutionary histories (see Fig. S1 in Supporting information): (1) Sierra de Guadarrama National Park (Guadarrama NP, hereafter; 40°47' N, 4°0' W), in central Spain, which is characterized by a typical Mediterranean climate with intense summer drought; (2) Ordesa-Monte Perdido National Park (Ordesa-Monte Perdido NP, hereafter; 42°40' N 0°03' E) in the central Pyrenees, within the same biogeographic region but with a temperate climate and without summer droughts; and (3) Farellones/Valle Nevado (33°20'S, 70°14'W) and Laguna del Maule (35°58'S, 70°30'W), in the central Chilean Andes, also characterized by a Mediterranean-type climate. Mean annual temperature and precipitation are 6.5 °C and 1350 mm in the Guadarrama NP (Navacerrada Pass weather station; 40° 47' N, 4° 00' W; 1894 m a.s.l.), 5 °C and 1660 mm in Ordesa-Monte Perdido NP (Góriz weather Station; 42° 39' N, 00° 01' E; 2215 m a.s.l.) and 6.5 °C and 943 mm in the central Chilean Andes (Cavieres et al., 2000; at 2300 m a.s.l.: Santibañez and Uribe, 1990), respectively.

We sampled vegetation above the treeline, in snow-free zones such as windblown slopes and crests, covering the complete elevation gradient in each mountain region. Elevation ranged from 1890 to 2420 m in Guadarrama NP, from 1650 to 2550 m in Ordesa-Monte Perdido NP, and from 2064 to 3627 m a.s.l. in the central Chilean Andes. The vegetation was consistently patchy and dominated by grasses together with creeping chamaephytes, perennial forbs and cushion-like plants in the three study sites. We sampled 39 sites during June and July of 2011 in Guadarrama NP, 27 sites during July of 2013 and 2014 in Ordesa-Monte Perdido NP, and 20 sites during January of 2014 in the central Chilean Andes. The sites represented a wide range of aspects and slopes along the local elevation gradient. We established in each site a sampling plot of 20 × 20 m in a relatively homogeneous vegetation area. Four 2.4 m × 2.4 m quadrats were established in the corners of the plot and a fifth in the centre. This sample size is large enough to represent the variation of this type of communities (see Pescador et al., 2015). All plant species and their percentage covers were visually estimated in each quadrat.

We calculated the potential solar radiation from the aspect (GPS: Garmin Colorado-300, Garmin Ltd., Olathe, USA) and the slope (clinometer: Silva Clinomaster, Silva Sweden, Sollentuna, Sweden) in each plot (Gandullo, 1974). Elevation was standardized by subtracting the treeline elevation value from plot elevation in the Chilean Andes (see López-Angulo et al., 2018b) since the sampled sites were distributed in different latitudes and the treeline was locally well-conserved. We collected one soil sample (5 cm in diameter and 10 cm deep) in the four corners of each plot. Soil samples were collected from bare areas to reflect the variations linked to abiotic differences among sites (Mihoč et al., 2016). The soil estimates of the centre quadrat were calculated as the average of the four quadrats at each site. Soil samples were air dried for one month and sieved through a 2 mm mesh. We measured soil total nitrogen because it is considered one of the main limiting nutrients in alpine ecosystems (Sundqvist et al., 2014). It was determined on a SKALAR++ San Analyzer (Skalar, Breda, The Netherlands) in the Nutrilab/URJC lab after digestion with sulphuric acid and Kjeldahl's catalyst (Anderson and Ingram, 1994). The central quadrat was regularly divided into 64 cells of 30 cm × 30 cm (8 × 8 cells). The presence of every plant species in each cell was recorded to calculate the checkerboard score (C-score: Stone and Roberts, 1990). We used the C-score as a surrogate for plant to plant interactions because this index quantifies the degree of aggregation for species co-occurrence (Dullinger et al., 2007). High C-score values indicate a tendency for species to spatially segregate which reveal prevalence of competitive interactions, and low values of this index would indicate species aggregation and facilitative processes (Dullinger et al., 2007).

### 2.2. Plant functional traits and measurements

Five functional traits were measured for most of the species in each mountain range. All these species represented 99% of the cover in Guadarrama NP, 94% in Ordesa-Monte Perdido NP and 87% in central Chilean Andes. However, we discarded the quadrats from the analyses when trait-assigned species accounted for <80% of the accumulated cover (16 from 135 and 22 from 100 quadrats in Ordesa-Monte Perdido NP and central Chilean Andes, respectively) to ensure a satisfactory description of functional community structure (Pakeman, 2014). (i) Vegetative height (VH, distance from the ground to the top of photosynthetic tissues) represents a trade-off between competitive vigour (Pérez-Harguindeguy et al., 2013) and protection by snow cover (Körner, 2003). (ii) Plant size (PS, canopy area projection) is a surrogate of the photosynthetic biomass and it is directly related to accumulated resources (Pescador et al., 2015). (iii) Specific leaf area (SLA, ratio of one-sided area of a fresh leaf divided by its dry mass) is correlated with relative growth and photosynthetic rates (Pérez-Harguindeguy et al., 2013). (iv) Leaf dry matter content (LDMC, oven-dried mass of a leaf divided by its fresh water-saturated leaf mass) is usually well correlated with resource investment in leaf tissues and with resistance to physical hazards (Pérez-Harguindeguy et al., 2013). (v) Leaf thickness (LT) is related to nutrient acquisition and resistance to wind (Choler, 2005). All these traits were measured in at least ten different well developed individuals per species, following the standard methodology of Pérez-Harguindeguy et al. (2013) with the exception of plant size, which was calculated as  $PS = \pi \cdot L \cdot S/4$  (Pescador et al., 2015), where L is the longest diameter and S is the shortest diameter perpendicular to the former one for each plant.

### 2.3. DNA sequencing and phylogenetic analyses

We constructed a phylogenetic tree using two barcoding loci (*rbcl* and *matK*) in order to estimate the phylogenetic diversity. We used a species pool composed of species found in the communities. Available species sequences from GenBank were downloaded (122 *matK* and 117 *rbcl* sequences) and the rest (771 sequences) were obtained in the Universidad Rey Juan Carlos lab. For that, fresh leaves from three

individuals per species were collected and were lately dry-stored in silica-gel for 1 month. Genomic DNA was isolated and extracted using the DNeasy Plant Mini Kit (QIAGEN, Valencia, CA, USA).

PCR amplifications of the *rbcL* barcode were performed in 25  $\mu$ L containing a reaction mixture of 2.5  $\mu$ L of Taq buffer 2 mM with MgCl<sub>2</sub>, 1  $\mu$ L of dNTP Mix (0.4 mM), 1.25  $\mu$ L of reverse and forward primer, 1.25 U Taq DNA Polymerase (Biotools, Madrid, Spain) and 2  $\mu$ L of genomic DNA. The *matK* barcode was amplified by puReTaq Ready-To-Go PCR beads (Amersham Pharmacia Biotech, Uppsala, Sweden). Primers for PCR, sequencing and PCR cycling conditions used in this study followed López-Angulo et al. (2018b). The subsequent products were clean-up using the ExoSap purification kit® (USB Corporation, Cleveland, OH, USA) and sequenced by Macrogen Inc. (Seoul, South Korea). Sequences were initially aligned using MAFFT online v. 7, and minor manual adjustment of the alignments was necessary only for the *matK* barcoding with Mesquite version 2.6. Maximum likelihood (ML) gene trees were calculated by the R-package 'Phangorn' (Schliep, 2011) in R v.3.5.1 using the GTR + G + I model and 100 bootstrap replicates (Violle et al., 2011).

#### 2.4. Diversity metrics and statistical analyses

We used species richness (the total number of species within each quadrat) as a measure of TD because it is a simple indicator of biological diversity and it has been the predominant measure of global biodiversity for a long time. We chose the mean pairwise distances (MPD) weighted by species abundance to estimate the functional and phylogenetic diversities because it is independent from species richness, unlike the very used Rao which can be correlated to number of species, especially at low levels of richness (de Bello et al., 2016). Distances among coexisting species were calculated using the Gower distance index to estimate FD and the cophenetic distance to estimate de PD. Before calculating the FD, we conducted a principal components analysis (PCA) using all the traits measured to control for correlations among traits and to define a multidimensional trait space for each mountain region (Devictor et al., 2010). The first two principal component analysis (PCA) axes (explaining between 72 and 81% of the trait variation for each mountain range: see Table S1 in Supporting Information) were retained for calculating FD. Trait data was log-transformed when necessary to reach normality and scaled prior to PCA analysis. The Gower matrix to calculate FD was estimated according to the selected PCA axes. Calculation of MPD was performed using the function "melodic" (de Bello et al., 2016).

We determined the phylogenetic signal for each individual plant trait (and the selected PCA components) to confirm phylogenetic niche conservatism when we found significant relationships between FD and PD. We tested the phylogenetic signal with the Pagel's  $\lambda$  using a Brownian motion model of trait evolution (Pagel, 1999), with the subset of species found in each mountain region. Pagel's  $\lambda$  was quantified using the 'phylosig' function in the Phytools package in R.

#### 2.5. Structural equation modelling

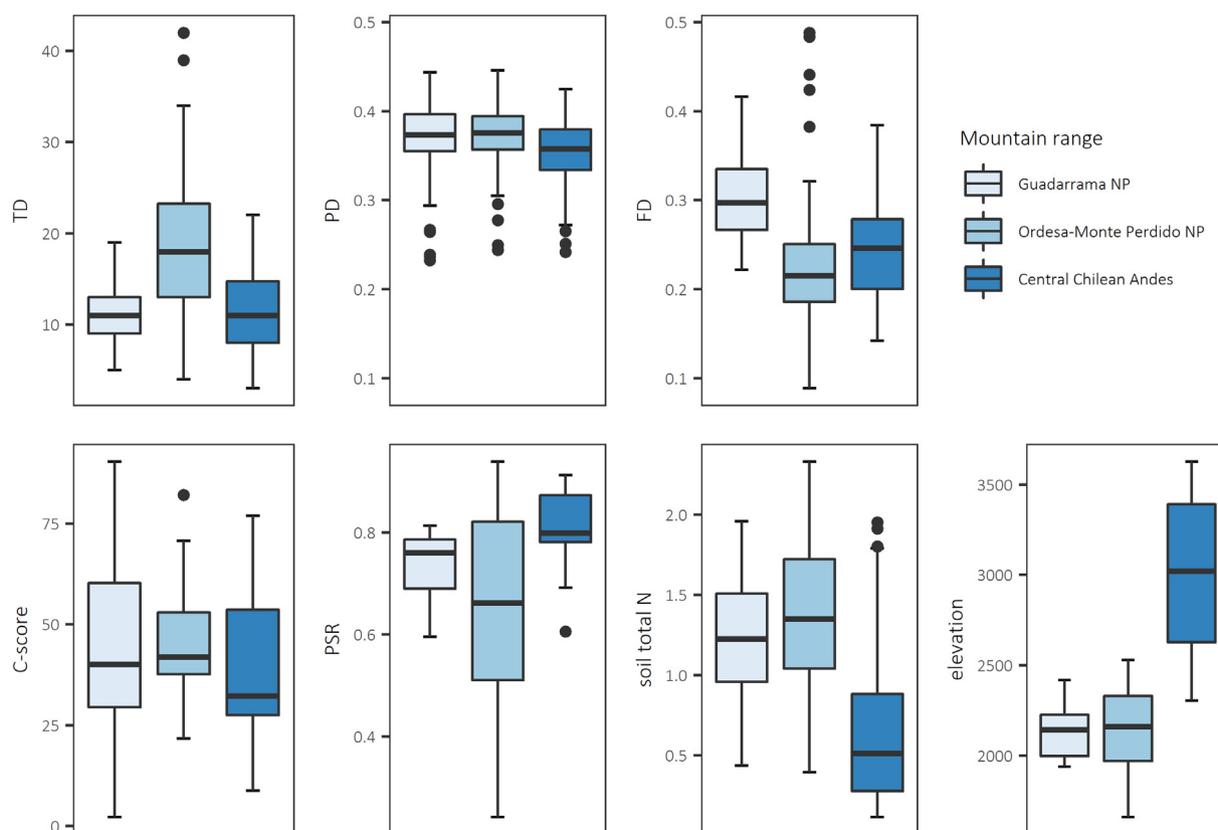
We evaluated the causal interplay between three diversity facets (FD, PD and TD), and abiotic (elevation, potential solar radiation and soil total nitrogen) and biotic determinants (C-score) using structural equation models (SEM: Grace, 2006). SEM allows testing causal links established in an initial hypothetical framework, comparing the observed variance-covariance structure with that expected if the proposed causal relationships are true. SEM takes into account the constraints imposed by the theoretical causal hypotheses with the observed variance-covariance structure (Grace, 2006; Iriondo et al., 2003; Maestre et al., 2005; for more details, see: Mitchell, 1992). If discrepancies are small, we can assume that the observed pattern in the data set is compatible with our hypotheses.

Our theoretical model proposes that each diversity facet can be shaped by different assembly mechanisms, and so, they will respond independently to abiotic conditions and to the intensity of plant-plant interactions, which depend on the level of abiotic harshness (see Cavieres et al., 2002) (Fig. 1). If the selected plant traits are phylogenetically conserved on the phylogeny, PD and FD would respond rather similarly to such environmental factors (Cavender-Bares et al., 2004; Swenson et al., 2007). In contrast, if the functional traits are not phylogenetically conserved we may expect different causal paths for both diversity facets where PD would reflect the response of other unmeasured traits with phylogenetic signal. TD is expected to be directly influenced by FD and PD, although these relationships will depend on the degree of functional redundancy in the selected traits (FD) and in the unmeasured traits (PD) (Petchev and Gaston, 2002). However, regardless of indirect effects on TD of environmental forces through FD and PD, we expect elevation, nitrogen in soil and biotic interactions to be critical determinants structuring species richness (TD) directly. This implies that TD might be affected by ecological determinants both directly or indirectly through FD and PD. Finally, we consider that environmental conditions could directly affect the prevalence of plant interactions (i.e. C-score) and consequently indirectly affect the interplay among facets of diversity. Since the relationships among environmental factors and the diversity facets could be specific for each mountain range, the proposed model (Fig. 1) was evaluated for each mountain region separately.

Standardized estimates of path coefficients were obtained using the maximum likelihood method because it is robust against certain deviations of multinormality (Shipley, 2000). They were used to interpret the scaling relationships among variables. Soil total nitrogen for Ordesa-Monte Perdido NP was log-transformed to reach normality a necessary step to reach multinormality. The discrepancies between observed and expected covariance matrices were first assessed by a chi-square goodness-of-fit statistic ( $\chi^2$ ). *P*-values above 0.05 indicate that the observed and the modelled covariances were not significantly different, suggesting adequate model fit. Since this test is prone to several statistical errors, especially when the sample size is large like in our case, we also used two additional measures of the goodness of fit: the comparative fit index (CFI) and the Bentler and Bonett's normed-fit index (NFI) (Iriondo et al., 2003) with values above 0.9 suggesting adequate fit. In order to minimize the risk of multicollinearity, we calculated the variance inflation factor (VIF) for each variable previous to analyses. We incorporated all variables in the models since all VIF values were <4 (Petraitis et al., 1996). SEM was conducted using the 'lavaan' package (Rosseel, 2012) in R.

### 3. Results

We registered 57 species in Guadarrama NP ( $n = 195$  quadrats), 153 species in Ordesa-Monte Perdido NP ( $n = 124$  quadrats) and 89 species in the central Chilean Andes ( $n = 78$  quadrats). The average number of species per quadrat (2.4  $\times$  2.4 m) was 10.9 ( $\pm 2.6$  SD) in Guadarrama NP and 11.2 ( $\pm 4.5$  SD) in the central Chilean Andes, being the richest mountain Ordesa-Monte Perdido NP with an average of 18.8 ( $\pm 7.7$  SD) species per quadrat. The five most frequent species in Guadarrama NP, *Festuca curvifolia* Lag. ex Lange, *Rumex angiocarpus* Murb., *Jurinea humilis* (Desf.) DC., *Sedum brevifolium* DC. and *Jasione crispa* (Pourr.) Samp. subsp. *centralis*, occurred at least in a 67% of the quadrats, whereas in Ordesa-Monte Perdido NP, *Thymus gr. serpyllum* L., *Koeleria vallesiana* (Honck.) Gaudin subsp. *vallesiana*, *Galium pyrenaicum* Gouan, *Festuca gautieri* subsp. *scoparia* (A. Kern. & Hack.) Kerguélen and *Helictotrichon sedenense* (DC.) Holub, and in the central Chilean Andes, *Poa gr. denudata* Steud., *Trisetum preslei* (Kunth) E. Desv., *Hordeum comosum* J. Presl, *Phacelia secunda* J.F. Gmel. and *Bromus setifolius* J. Presl, were registered in 36% and 32% of the quadrats, respectively. The plant communities located in Guadarrama NP showed higher average values of FD than in Ordesa-Monte Perdido NP and the central Chilean Andes (Fig. 2, Table S2 in Supporting information), while the



**Fig. 2.** Boxplots summarizing taxonomic (TD), phylogenetic (PD), functional (FD) diversity and the predictor variables (elevation, potential solar radiation, soil total nitrogen and C-score) per mountain range. Abbreviations: TD, taxonomic diversity; PD, phylogenetic diversity; FD, functional diversity; C-score, checkerboard score; PSR: Potential solar radiation; soil total N, soil total nitrogen.

average values of PD were close to 0.36 in the three mountain ranges. There were important differences between regions in the abiotic variables measured. The average values of elevation and potential solar radiation were higher in the central Chilean Andes compared to the other two mountain ranges (Guadarrama NP and Ordesa-Monte Perdido NP) (Fig. 2). However, the soil total nitrogen levels in the central Chilean Andes, where soil is derived from metamorphic volcanic substrates, were two times lower ( $0.6 \text{ mg g}^{-1}$ ) than in soils of the two Spanish locations ( $>1.2 \text{ mg g}^{-1}$ , see Table S2).

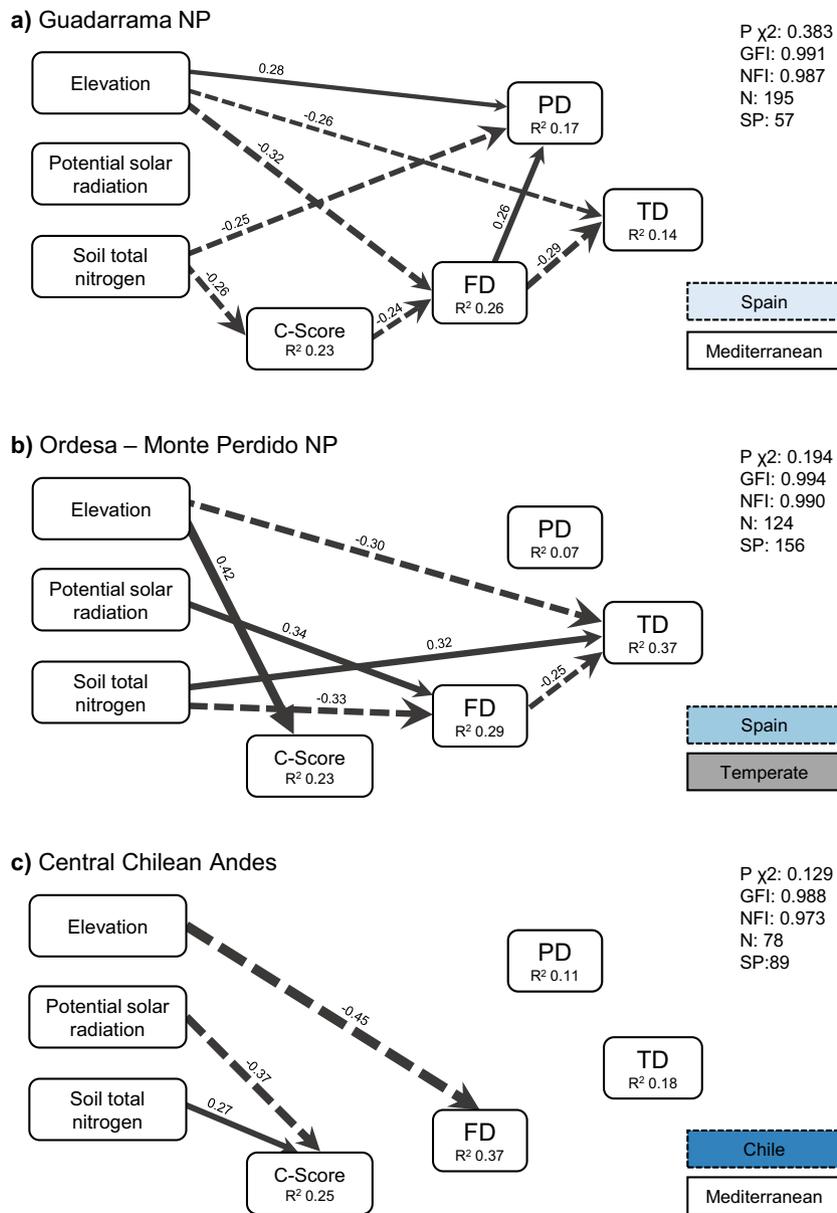
Our hypothetical causal model was significant in the three mountain ranges but with very different significant relationships among the different variables on each region (Fig. 3a, b, c), so a multisample analysis was not necessary. The model for Guadarrama NP provided a good fit to observed data as indicated the non-significant  $\chi^2$  ( $\chi^2 = 3.83$ ,  $DF = 1$ ,  $P = 0.051$ ), and the values of NFI and GFI higher than 0.98 (Fig. 3a). The SEM model explained 26, 17 and 14% of the variance in FD, PD and TD, respectively (Fig. 3a). Overall, the three diversity facets were differently affected by the considered ecological determinants. Elevation was the most important abiotic determinant in Guadarrama NP, since all diversities were significantly influenced by this variable. Specifically, elevation negatively affected FD and TD ( $r = -0.32$  and  $r = -0.26$ ), in spite of the negative relationship found between these two diversity facets (FD and TD,  $r = -0.29$ ). In contrast, PD was positively influenced by elevation even when a positive relationship between FD and PD ( $r = 0.26$ ) was found. Soil total nitrogen negatively influenced PD and C-score. Finally, it is important to note that C-score modified plant diversity only in Guadarrama NP, where species aggregation lead to communities with functionally dissimilar species.

The model for Ordesa-Monte Perdido NP also showed high statistical support, as indicated by non-significant  $\chi^2$  values ( $\chi^2 = 1.69$ ,  $DF = 1$ ,  $p = 0.194$ ) and by values of NFI and GFI also higher than 0.99, indicating

that field data adjusted to the theoretical causal model (Fig. 3b). This SEM model explained around one-third of the variance in both FD and TD ( $R^2 = 0.29$  and  $0.37$  respectively) but had little explanatory power for PD ( $R^2 = 0.07$ ). In contrast to the results for the Guadarrama NP model, soil total nitrogen made the largest contribution to the diversity facets, negatively affecting FD ( $r = -0.33$ ) but positively TD ( $r = 0.32$ ). Elevation also exerted an important negative effect on TD ( $r = -0.30$ ). TD was again negatively influenced by FD (Fig. 3). No relationships between biotic or abiotic determinants and PD were found in Ordesa-Monte Perdido NP (Fig. 3b).

Finally, the model for the central Chilean Andes fitted the observed data correctly as indicated by the goodness-of-fit statistics (Fig. 3c) and was able to explain nearly double of the variance in FD ( $R^2 = 0.37$ ) than in TD and PD ( $R^2 = 0.18$  and  $0.11$  respectively). In the Central Chilean Andes, an exclusive and strong significant relationship between elevation and FD ( $r = -0.45$ ) was detected. Despite the strong causal relationships between soil total nitrogen and potential solar radiation with the surrogate of biotic interactions (C-score, Fig. 3c) no other relationships with diversity facets were found.

Total effects (sum of direct and indirect effects; see Table S3 in Supporting information), showed that elevation had a negative total effect on TD in all mountain ranges (Fig. 4). Elevation also moderately affected FD and C-score in both Mediterranean-type mountain ranges, while in the temperate Ordesa-Monte Perdido NP the opposite pattern was found (Fig. 4). However, the total effects of elevation on PD were positive in Guadarrama NP, but negative in Ordesa-Monte Perdido NP and central Chilean Andes (Fig. 3). When the relationships among the diversity facets were evaluated, the total effects revealed a positive relationship between FD and TD ( $r = 0.34$ , Table S3) in the central Chilean Andes, contrasting with the results found in both Spanish mountain ranges (Guadarrama NP and Ordesa-Monte Perdido NP; Fig. 3). In



**Fig. 3.** SEM models for a) Guadarrama NP in central Spain, b) Ordesa-Monte Perdido NP in central Pyrenees and c) central Chilean Andes. Positive effects, solid blue lines; negative effects, broken orange lines. Arrow widths are proportional to standardized path coefficients. Path coefficients non-significantly different from zero were omitted. R<sup>2</sup> denotes the proportion of variance explained and appears below every response variable in the model. Goodness-of-fit statistics (P  $\chi^2$ , GFI and NFI), sample size (N) and number of species (SP) are provided at the upper-right corner of each diagram. Abbreviations: TD, taxonomic diversity; PD, phylogenetic diversity; FD, functional diversity; C-score, checkerboard score. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

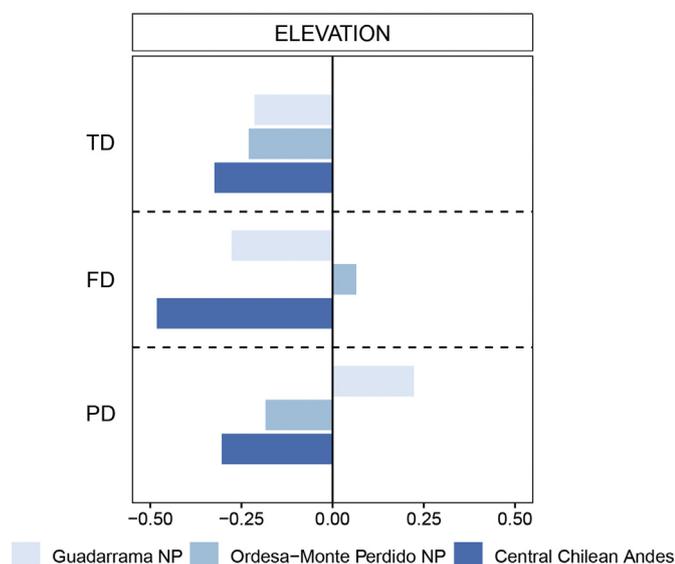
spite of the fact that the PCA axes obtained from the plant functional traits showed a relatively strong phylogenetic signal across the three mountain ranges (Table S4 in Supporting information), we only found an important effect of FD on the variation of PD in Guadarrama NP (Fig. 3a).

**4. Discussion**

Our aprioristic causal model of relationships among different diversity facets (TD, FD and PD) together with some critical biotic and abiotic determinants resulted significant in three mountain ranges differing in climate (Mediterranean vs temperate), and in evolutionary history (Spain vs Chile). Although numerous studies have shown that some abiotic factors independently shaped diversity in terms of taxonomic, functional or phylogenetic properties (Bernard-Verdier et al., 2013; Dainese et al., 2015; Hurtado et al., 2019; Oliver et al., 2013), this study

represents a first attempt to define how the abiotic environment, together with plant-plant interactions, determine the interplay among the TD, FD and PD in different alpine plant communities. Our results provided empirical support not only for the direct relationships among the studied abiotic and biotic determinants with the different diversities of these alpine communities but also revealed that the indirect effect of elevation can modify such direct links an issue that has gone still unnoticed. Noteworthy, these findings supported our hypothesis that FD plays a key role in community assembly affecting, lately, the other diversities, because the FD directly and strongly responds to environmental factors, and in turn, it affects globally the community structure through the effect on the other diversity facets.

Significant causal links varied among mountain ranges with shifts from positive to negative in one compared to other mountain ranges (e.g., soil total nitrogen vs C-score in both Mediterranean mountain ranges) which suggests strong context-dependence (Cadotte et al.,



**Fig. 4.** Standardized total effects (sum of direct and indirect effects) of elevation on the three diversity facets (TD, FD, PD) in the three mountain ranges (Guadarrama NP, Ordesa-Monte Perdido NP, and the central Chilean Andes). Abbreviations: TD, taxonomic diversity; PD, phylogenetic diversity; FD, functional diversity.

2011). For example, in Ordesa – Monte Perdido NP, soil total nitrogen exerted a strong negative effect on FD, but a positive effect on TD, whereas in Guadarrama NP, the phylogenetic facet positively responded to increases in nitrogen, and in the central Chilean Andes no effects of soil nitrogen on any diversity facets were found. The existence of a unimodal response of plant diversity to long soil fertility gradients is well-established (Grime, 2006). However, our results suggest that in nutrient-limited systems, such as alpine ecosystems (Körner, 2003; Sundqvist et al., 2014), the relationship between TD and soil total nitrogen in Ordesa – Monte Perdido NP could represent the ascending side of the curve. Thus, increases of the soil total nitrogen might lead to the release of species with narrow tolerance increasing the number of species (Fox, 1992; Laliberté et al., 2014; Theodose and Bowman, 1997) as described in other temperate mountains. However, the negative relationship with FD in this temperate mountain (i.e., Ordesa – Monte Perdido NP) suggest that plant assemblages in more fertile soils (in relative terms) presented more functionally similar species. This result may be related to the dominance of species with functional traits that confer higher competitive ability (Fox, 1992). In Guadarrama NP, the increases of soil total nitrogen also led to competitive dominance, but in this case, of phylogenetically related species.

We found a consistent negative pattern of TD with increasing elevation except in the central Chilean Andes. The absence of this direct relationship (between elevation and TD) in this mountain range could be due to the fact that this relationship is unimodal (López-Angulo et al., 2018a). However, when focusing on the total effects (sum of direct and indirect effects; Table S3), TD diminished in the uppermost elevation limit in the three regions, being the total elevation effect stronger in the central Chilean Andes. This drop of TD is one of the most commonly reported patterns of diversity for alpine environments (Colwell et al., 2004; McCain and Grytnes, 2010; Rosenzweig, 1995; Sanders and Rahbek, 2012). The decay in richness is usually accompanied by low levels of FD (de Bello et al., 2013; Read et al., 2014) such as we found in both Mediterranean-type mountains, due to the limitations imposed by coldness (which increases in magnitude and duration with elevation) that restricts the viable trait range, and limits the number of plant species established in such stressful environments (Cornwell et al., 2006; Weiher and Keddy, 1995).

FD was the unique metric that responded directly to the environment in the three mountain ranges, supporting our expectation that the species integrating realized assemblages mainly respond to ecological pressures on the basis of their functional traits. Thus, as hypothesized the functional configuration of communities is critical to understand the community assembly (Diaz et al., 1998; Shipley et al., 2016; Weiher and Keddy, 1995). Moreover, a substantial fraction of the total variance of TD, 25% to 31%, was determined by FD in all mountain ranges, although the total effects shifted from negative in both mountain ranges of Spain to positive in the central Chilean Andes. This result is congruent with our hypotheses, not only that FD responds first and stronger than other diversity facets to environment, but also that FD plays a critical role in structuring the whole diversity of the communities. We are aware that other researchers, however, found that TD represents the diversity facet that determines FD, showing a positive trend between them (Cadotte et al., 2011; Flynn et al., 2011; Pavoine et al., 2013; Petchey and Gaston, 2002). The idea that an increase in species number causes a similar increase in FD rests on the premise that the trait values of species are distributed uniformly along the total length of the local functional space (i.e., co-occurring species have complementary strategies and contribute proportionately to the functional diversity of communities) (Petchey and Gaston, 2002). However, the negative relationship between FD and TD in Guadarrama NP and Ordesa-Monte Perdido NP contrasts with this intuitive hypothesis, higher FD values are associated to higher species richness (Petchey and Gaston, 2002) failing thus to support the niche complementary hypothesis (Loreau, 2000). As suggested by Cadotte et al. (2011) ecological redundancy may drive the negative relationship between these two diversity facets (Cadotte et al., 2011), which mainly occurs in species rich assemblages (Loreau, 2004; Naem, 1998). Similar to our results, de Bello et al. (2009) found an increase in functional redundancy associated to an increase in taxonomic diversity in alpine pastures in the Catalanian Pre-Pyrenees. Our results indicate that the volume of trait space was occupied by a few species, and when species richness increased, the new species were not functionally different from those already present (Díaz and Cabido, 2001). The consistency of the relationship across regions sharing regional species pool and similar evolutionary histories is particularly interesting, and although these results need further investigation, they suggest the existence of symmetries in the evolutionary forces regulating the volume of trait space in the regional species pool. Worth also to note that unlike the sum of distances based-metrics (i.e. Faith's Index) which generally increase with richness (Díaz and Cabido, 2001; Petchey and Gaston, 2002; Swenson, 2014), the mean pairwise functional distance-based metrics (unaffected by richness) such as the MPD, allow to decrease when a redundant species enters into the community. Thus, the choice of adequate measures of FD is critical to correctly evaluate the relationship between the taxonomic and functional facets (Cadotte et al., 2011). Worth also to note that the role of the FD in the assembly may vary depending on the trait considered when calculating the FD metric.

Our results also showed few significant relationships in which PD was involved. In accordance with previous studies, this suggests that PD is a poor indicator of assembly processes at the ecological time scale (Gerhold et al., 2015; Pavoine et al., 2013). However, it is noteworthy that in Guadarrama NP the increase in elevation generated an increase in PD opposite to the decline in FD, in spite of the fact that PD was positively correlated with FD, which was consistent with the strong phylogenetic signal found in the considered functional traits. Although a decrease in PD has generally been described in the literature with elevation (Bryant et al., 2008; Graham et al., 2009; Machac et al., 2011) specially in the case of plants (Li et al., 2014; Xu et al., 2017), discrepancies between the functional and phylogenetic diversities have also been reported in high-elevation grasslands in the European Alps (Dainese et al., 2015). One potential explanation of this apparent discrepancy is that an increase in intensity and importance of facilitation is expected under harsher environmental conditions (Anthelme et al., 2012; Brooker

et al., 2008; Callaway et al., 2002), and according to Valiente-Banuet and Verdú (2007), when facilitation drives the assembly of plant communities, an increase in PD is expected. In our study, the increase in facilitation intensity was supported by the fact that elevation led to low levels of the C-score values (at least when focusing on the total effects;  $r = -0.176$ , Table S3), that can be interpreted as a higher prevalence of positive interactions among plants with increasing altitude (Dullinger et al., 2007; Schöb et al., 2013). Furthermore, the role of the biotic interactions was mainly involved in modulating the relationship between the soil total nitrogen and the FD in Guadarrama NP. So, low levels of soil total nitrogen favoured a segregated pattern of species co-occurrence, which in turn led to a decline in FD. This suggests that the influence of competitive interactions on the local assembly processes increases in soils with lower nitrogen availability. Under these adverse conditions, species tend to be functionally similar to favour those advantageous strategies allowing access to nitrogen (Lambers et al., 2008; Mason et al., 2012). However, with higher soil total nitrogen availability, coexisting species tend to have different ecological requirements (i.e., higher FD) to be spatially aggregated (i.e., lower C-score values) providing support for niche differentiation among species (Kikvidze et al., 2005; MacArthur and Levins, 1967; Stubbs and Wilson, 2004).

A remarkable finding of this study is that ecological determinants such as soil total nitrogen and elevation alter the relationships between the three components of diversity. This effect varied in sign, exacerbating or mitigating the direct relationship between the diversity components. For instance, the direct negative link between FD and TD in Ordesa-Monte Perdido NP was exacerbated by the opposite indirect effect of soil total nitrogen on FD and TD. Conversely, in Guadarrama NP, the positive relationship between FD and PD was mitigated due to opposing effects that elevation exerted on these diversities. In addition, elevation mitigated the strength of the negative relationship between FD and TD, since changes in elevation generated shifts of functional and taxonomic diversity in the same direction.

Disentangling the interplay among the diversity facets and their variation across different mountain ranges with contrasting evolutionary histories and climatic conditions provides unique insights about the mechanisms that shape community structure in alpine communities. Our study provides evidences for the already known important role of elevation gradient in maintaining and generating diversity in these alpine plant communities. However, our results call for caution when extrapolating local assembly processes to other mountains even if they share important features such as climate and/or biogeographic similarities, due to the idiosyncratic nature of the observed relationships. Our results also highlight that natural communities mainly respond to ecological pressures on the basis of their functional structure, which in turn has a causal influence upon the phylogenetic and taxonomic community structures. In spite of species richness and phylogenetic structure do not encompass all aspects of functional community structure (Bernard-Verdier et al., 2013; Díaz and Cabido, 2001; Mouchet et al., 2010), our study highlights that TD and PD also capture different and complementary information, so respond to different ecological factors leaving identifiable signatures on community assemblage processes. Therefore, we encourage to consider not only the functional diversity facet but also the taxonomic (almost forgotten in later years) and the phylogenetic information.

#### CRedit authorship contribution statement

**Jesús López-Angulo:** Data curation, Formal analysis, Investigation, Software, Visualization, Writing - original draft. **David S. Pescador:** Investigation, Methodology, Writing - review & editing. **Ana M. Sánchez:** Investigation, Writing - review & editing. **Arantzazu L. Luzuriaga:** Investigation, Writing - review & editing. **Lohengrin A. Cavieres:** Conceptualization, Funding acquisition, Writing - review & editing. **Adrián**

**Escudero:** Conceptualization, Funding acquisition, Methodology, Software, Supervision, Writing - review & editing.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Acknowledgements

We thank Carlos Diaz, Maritza Mihoc, and Cristina Contreras for technical assistance in the field, and Pilar Hurtado for her help in the SEM analyses. This study was supported by the Spanish Ministry of Economy and Competitiveness under the ROOTS project [CGL2015-66809-P], the Madrid Autonomous Community under the REMEDINAL TE project (P2018/EMT-4338). JLA was supported by a post-doctoral contract (M1718-178) from the Ministry of Education, Youth and Sports, Government of Madrid and the European Social Fund, and by a visiting researcher grant EEBB-I-17-12091 from the Ministry of Science and Innovation. LAC acknowledges grants FONDECYT 1171005 and CONICYT-PIA AFB 170008. DSP was supported by the Spanish Ministry of Economy and Competitiveness through the EU BiodiverSA-funded project DIGGING\_DEEPER (ref. PCIN-2016-028).

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.133960>.

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