**Scale-dependent effects of plant diversity drivers in grasslands**

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**Abstract**

Understanding what governs grassland biodiversity across different spatial scales is crucial for effective conservation and management. However, current evidence often focuses on single sampling grain sizes, leaving the mechanisms of biodiversity drivers and their scale-dependency unclear.

Here, we investigated the impact of potential biodiversity drivers (climate, soil properties, abiotic disturbance, and land use) on plant diversity across fine spatial scales in various grassland types. We collected spatially explicit data on species presence, relative cover, and total community cover at two grain sizes (**α**- and **γ**-diversity) to assess the mechanisms driving scale-dependent diversity patterns (**β**-diversity).

In our study, the most influential factors of plant diversity at both scales (grain sizes) were climate variables, followed by soil humus content, litter cover, and soil pH. The effects of soil and litter were primarily driven by the response of rare species, while climate and grazing effects were driven by locally common species. The strength of most of these effects varied between spatial scales and therefore affected **β**-diversity.

We identified three key mechanisms through which these drivers affect the scale-dependency of biodiversity: total plant cover, species relative cover (commonness or rarity of species and species evenness in the community), and species intraspecific aggregation. Climate effects operated through changes in species relative cover and intraspecific aggregation. Soil humus influenced **β**-diversity by altering the total cover of the plant community and by increasing intraspecific aggregation, resulting in stronger effects of soil productivity on plant diversity at larger than smaller spatial scales. Microhabitat patchiness by litter cover altered distributions in the relative cover of species due to reduced asymmetric competition, and affected the total cover of the plant community.

Our findings support the idea that the responses of biodiversity to climate, soil factors, and litter depend on the size of the sampled area. We have identified main mechanisms behind the scale-dependency of biodiversity drivers and highlighted the significance of locally rare and common species. Our results underscore the importance of incorporating the scale-dependency of biodiversity drivers in conservation efforts, management strategies, and analyses of global change impacts, which would enhance our ability to predict potential biodiversity change.

**Keywords**: biodiversity, spatial scale, grasslands, biodiversity drivers.

**1. Introduction**

The variability in the numbers of species that occur and persist in a given area, known as biodiversity, remains one of the most well-studied but poorly understood phenomena in ecological investigation (Díaz & Malhi, 2022; Hillebrand et al., 2018). Environmental drivers, such as climate, edaphic factors (Sala et al., 2000; Ulrich et al., 2014), and land use (Díaz et al., 2019; Newbold et al., 2015; Sala et al., 2000), can play a critical role in determining biodiversity. However, differences in the grain size (hereafter scale) at which biodiversity is quantified (Chase et al., 2018; McGill, 2010a), as well as the metrics by which it is measured (Chao et al., 2014; Jost, 2006), can dramatically influence our conclusions about the importance of these drivers for biodiversity change (Field et al., 2009; Siefert et al., 2012). The limited understanding of the scale-dependency of biodiversity drivers and their underlying mechanisms hampers the translation of findings from local-scale experiments and observations to larger spatial scales relevant to management, conservation, and restoration policies (Barton et al., 2013; Chase et al., 2019; Ladouceur et al., 2023; Primack et al., 2018; Smith, 2010). It also impairs our ability to accurately predict biodiversity alterations under ongoing and future global changes (Sala et al., 2000), as well as their consequences for ecosystem functions and services (Buzhdygan, Meyer, et al., 2020).

Spatial variability in composition of grassland plant communities is particularly high at fine spatial scales (<100 m2) (Biurrun et al., 2021), which are commonly used for sampling grassland vegetation (Chytrý & Otýpková, 2003). At the same time, at fine scales, grasslands are remarkably species-rich and often have even higher plant diversity than tropical forests (Biurrun et al., 2021; Wilson et al., 2012), especially in temperate regions (Dengler et al., 2020). For example, a site in Ukraine had 119 species in 16 m2 (Roleček et al., 2019), a site in Romania had 98 species in 10 m2 (Wilson et al., 2012), and another grassland site in Ukraine had up to 12 species in 1 cm2 (Moysiyenko et al., 2022). Many of these plant species are grassland specialists and many are endemic to specific regions or grassland types, making them rare or endangered. Despite their high biodiversity, temperate grasslands are among the most threatened ecosystems due to global change and are among the least protected ecosystems globally (Petermann & Buzhdygan, 2021). Understanding the factors that govern grassland biodiversity has, therefore, been a major focus of research in recent decades. However, the responses of grassland plant diversity along natural and anthropogenic gradients tend to be highly dependent on the spatial scale at which data were collected and analyzed (Dembicz, Dengler, et al., 2021), and such scale-dependency was reported for different grassland types and regions. For example, the effects of climate variables, such as precipitation or temperature, increased with the sampling grain in steppe grasslands in Ukraine (Kuzemko et al., 2016) and Iran (Talebi et al., 2021), dry grasslands in Bulgaria (Dembicz, Velev, et al., 2021), and Swiss inner-alpine valleys (Bergauer et al., 2022). Similarly, the scale-dependency of soil effects, such as pH, moisture, nutrient and humus content, has been reported for seminatural dry grasslands (Auestad et al., 2008; Dembicz, Velev, et al., 2021; Turtureanu et al., 2014). Various types of land use, such as, grazing in pastures in Spain (de Bello et al., 2007), mowing in seminatural dry grasslands in Romania (Turtureanu et al., 2014), burning in steppes in Ukraine (Kuzemko et al., 2016), fertilization in various grassland types across North America (Chalcraft et al., 2008), the Palaearctic region (Dembicz, Dengler, et al., 2021), and the globe (Seabloom et al., 2021), as well as overall land-use intensity in seminatural grasslands in Norway (Auestad et al., 2008), Germany (Bolliger et al., 2024), and alpine grasslands across Europe (Spiegelberger et al., 2006), have all been found to have scale-dependent effects. However, most of the existing evidence is limited to specific grassland types and usually varies in terms of sampling scales. This hinders our ability to test the generality and consistency of the scale-dependency of biodiversity drivers across different grassland habitats at macroecological spatial extents (Biurrun et al., 2021). For example, this includes the commonly accepted assumption that edaphic drivers dominate at smaller spatial scales, while climate and land use have a greater impact at larger scales (Auestad et al., 2008; Bergauer et al., 2022; Dembicz, Velev, et al., 2021; Kuzemko et al., 2016; Olagoke et al., 2023; Talebi et al., 2021; Turtureanu et al., 2014). Although some grassland studies contradict these patterns (e.g., Polyakova et al. 2016) and agree with the opposite assumption that grassland management has a dominant effect at smaller scales while species pool effects dominate at larger scales (Chytrý et al., 2015).

Scale-dependent effects of ecological drivers emerge when the influence of a given driver depends on the sampling grain or extent in which diversity is measured. This can occur when the driver influences species densities within a community (total abundance of individuals per area), species relative abundances (commonness or rarity of species and species evenness in the community), or spatial aggregation of species within a landscape (Chase et al., 2018; Chase & Knight, 2013; McGill, 2011; Storch, 2016). An area with more individuals generally has more species, which is sometimes called the more individuals effect (Srivastava & Lawton, 1998). Therefore, higher species population densities are expected to increase species richness across spatial scales (Gaston, 2000). However, at the fine grains the space limitation can cause an asymmetric competition among densely populated plant communities, thus often leading to lower species richness at smaller scales than at larger ones (Storch, 2016). Higher evenness of species relative abundances within the community increases richness at small spatial scales, thus leading to lower variability of species richness across spatial scales (Chase & Knight, 2013). In contrast, increased spatial aggregation (clustering of conspecifics) reduces richness at small scales because aggregated species are less likely to be encountered at limited area. But, as area increases, the effect of intraspecific aggregation becomes weak due to higher probability to sample the aggregated species (Chase & Knight, 2013). In any case where the driver alters the total or relative abundances of species, or their propensity to aggregate, the relationship between smaller (**α-**) and larger (**γ-**) scales can change measures of **β-**diversity **─** the spatial variability of biodiversity, where **β** = **γ** / **α** (Whittaker, 1972).

The uncertainty in understanding the diversity change across spatial scales is fuelled by the choice of metrics by which biodiversity is quantified (Chase & Knight, 2013). The majority of previous studies in grasslands used species presence-absence data at multiple sampling grains, for example to compare species richness across different scales or to construct and compare slopes and intercepts of species**-**area curves across environmental gradients (Bergauer et al., 2022; Dembicz, Velev, et al., 2021; Kuzemko et al., 2016; Talebi et al., 2021; Turtureanu et al., 2014). These studies provide important information on the relative importance of ecological drivers in governing species richness at different scales. However, the presence–absence data, and the species richness alone, cannot reflect changes in species densities (Hillebrand et al., 2018), thus not allowing an explicit consideration of the possible mechanisms that underlie shifts in **β-**diversity, such as altered total or relative abundances of species or via intraspecific aggregation (Blowes et al., 2022; Chase & Knight, 2013; He & Legendre, 2002; Tjørve et al., 2008). Furthermore, the species richness measure strongly depends on species pool (Chase & Knight, 2013). Thus, by solely focusing on the responses of species richness to scale across different grassland habitats may overestimate the effects of biodiversity driver and their scale-dependency, due to the differences in species pools among the habitats (Kraft et al., 2011). Instead, using spatially explicit data on total and relative abundances of species in the community allows to decouple the importance of species abundance distribution (rarity and commonness of species) and intraspecific aggregation as the mechanisms by which an ecological driver influences biodiversity patterns across scales (Chase & Knight, 2013). Despite the development of a formal theory that integrates these mechanisms and links them to biodiversity drivers (e.g., McGill 2010b, Chase and Knight 2013, May et al. 2018, Storch et al. 2018), and its recent adaptation to the nested fine-scales for grassland plant diversity (Dembicz, Dengler, et al., 2021), these mechanisms have rarely been tested for different biodiversity drivers in grasslands (e.g., DeMalach et al. 2019). Such a mechanistic understanding is important because depending on the mechanism through which the biodiversity drivers operate, they can shift the direction of their effects (Bergauer et al., 2022; Kuzemko et al., 2016) or change the shape of the effects with scale (Chase & Leibold, 2002; Šímová et al., 2013). Furthermore, the role of the responses of locally rare species in these mechanisms remains not clear.

Here, we explore the effect of potential drivers of plant diversity in grasslands, such as climate, soil properties, litter cover, and land-use management. We test the scale-dependency of these drivers and the mechanisms that may underlie their effects. For this, we use spatially explicit data on the relative cover of each plant species (vascular and non-vascular) in the community sampled at two grain sizes (10 m2 as **α**-scale and 100 m2 plots as **γ**-scale) in all grassland habitat types in Ukraine. Such data are strongly underrepresented in international research initiatives, similarly to other countries in Eastern Europe, thus limiting our ability to support appropriate management and conservation efforts in these regions (Chytrý et al., 2019). For example, Ukrainian grasslands, which are among the world plant diversity hotspots (Kuzemko et al., 2016; Moysiyenko et al., 2022), are still understudied compared to other grassland regions, especially unique natural grassland habitats, such as Ukrainian steppes (Borovyk et al., 2023; Kuzemko et al., 2016). Studies of scale-dependency of biodiversity drivers in Ukrainian grasslands are scarce and focused only on single grassland types (Borovyk et al., 2023; Kuzemko et al., 2016). Closing the geographical gaps for such data would help us to respond more effectively to the global ecological and societal challenges (Chytrý et al., 2019). For example, current data are the biodiversity records before the ongoing military actions in Ukraine that are dramatically affecting these unique grassland habitats (Skobel et al., 2023). Understanding biodiversity drivers and their spatial variability in these habitats will help to assess the environmental impact of the war and plan the future restoration of these ecosystems. Specifically, in this study we address the following questions:

1. Which ecological drivers affect local plant diversity (**α**- and **γ**-scale), and do these effects result from the responses of common or locally rare species?
2. Do the effects of biodiversity drivers depend on the sampled grain?
3. Is the scale-dependency of the effect of an ecological driver on plant diversity (**β**-diversity) mediated by the altered species density, changes in relative abundances (rarity or commonness of species), or intraspecific aggregations?

**2. Materials and Methods**

**2.1 Study area**

**2.1 Study area**

We sampled grasslands of all major grassland habitat types of Ukraine (Table S1) –(Kuzemko et al., 2022). All plots were sampled in Ukraine during 2010-2022, resulting in 11 datasets (see Table S1). The geographical extent of the data covered an area from 46.08° N to 51.87° N and 24.2° E to 37.76° E and an elevational gradient from 0 m to 1805 m a.s.l. (Fig. 1a).

The average annual temperature in the study area ranges from 0.3 °C to 11.4 °C (Karger et al., 2018). In the North, the average January temperature ranges from -3 °C to -2 °C, while in the South, it ranges from -2 °C to -1 °C. The average July temperature in the North ranges from +18 °C to +21 °C, and in the South, it ranges from +23 °C to +25 °C. In the Carpathian region, the average annual temperature on the upper belts is about 7–10 °C. In the mountains, the average January temperature ranges from -10 °C to -8 °C, and in July, the average temperature at an altitude of 1500 m a.s.l. is about 10 °C. The annual precipitation range is 700–800 mm in the Northern part of the study area (Volyn region and Rivne region), and 400–550 mm per year in the South (Mykolaiv and Kherson regions). The Carpathians have significantly higher levels of precipitation, reaching up to 1600 mm at an altitude of 1500–1800 m a.s.l. (Buzhdygan, Tietjen, et al., 2020).

**2.2 Plot design, sampling, and biodiversity predictors**

The study plots were established in homogenous environmental conditions and within a single grassland habitat type. Sampling design was based on the standard sampling methodology (Dengler et al., 2016) of the Eurasian Dry Grassland Group (EDGG, <https://edgg.org>). Each plot of 100 m2 (n=174) included two 10 m2 subplots (n=348) situated in opposite corners (Fig. 1a). Within each plot and subplot, we recorded all species of vascular plants, terricolous bryophytes and lichens. Study grasslands were selected to cover all possible grassland habitat types according to the EUNIS system v.2018 (Schaminée et al., 2018). The habitat types were preliminarily identified in the field with subsequent verification using the EUNIS-ESy expert system at 3rd level of hierarchy (Chytrý et al., 2020). But for the propose of this study we assigned these habitats type to the groups which correspond to the 2nd level of the EUNIS hierarchy: dry, mesic, wet, alpine, fringe, saline. One of the study grasslands – the depressions (*pody*) of the steppe zone, is not currently in the EUNIS-ESy expert system. It was identified based solely on the environmental characteristics (Shapoval & Kuzemko, 2021). We classified *pody* as habitat complexes group, which are defined as the heterogeneous combinations of different habitat types that can coexist at the same location over time or occur across spatial mosaics (Evans, 2016). The taxonomic nomenclature for vascular plants followed the Euro+Med (2006+), for bryophytes (Hodgetts et al., 2020) and for lichens (Kondratyuk et al., 2021). For each plant species we recorded its estimated cover in percent (Dengler & Dembicz, 2023).

At each plot we recorded litter cover, level of grazing intensity, and presence/absence of mowing. In each 10-m2 sub-plot, we took soil samples from the upper 10 cm of the soil surface in five random locations. Level of grazing intensity (ordinal variable with 4 levels) was estimated in field ranging from 0 – no grazing, to 3 – intensive grazing. We measured soil pH electrometrically in a suspension of 5 ml soil with 25 ml deionised water. Soil organic carbon was measured for each sample using 0.4 N potassium dichromate solution in accordance with Tyurin’s method. Litter cover in grasslands indicates productive communities that develop with moderate disturbances and not extremely harsh environmental conditions (Facelli & Pickett, 1991; Grime, 1979). However, a major management problem associated with abandonment of highly productive grasslands is the increase in above-ground biomass and the subsequent litter accumulation (Ruprecht et al., 2010), which, in excessive amounts, becomes disturbance to plant community assembly processes (Facelli & Pickett, 1991; Ruprecht & Szabó, 2012). Therefore, litter cover can be considered as an indication of productivity (high levels) and as an proxy of disturbance at both low litter cover (Dembicz, Dengler, et al., 2021) and high litter cover (Ruprecht et al., 2010; Ruprecht & Szabó, 2012). Land use is considered an anthropogenic disturbance. High and low levels of soil pH represent factors of soil-related stress to the plant community, as well as soil toxicity to plants at low pH. Soil organic carbon indicates site productivity for the grassland plant community.

For each 100-m2 plot, using plot coordinates, we extracted the following climatic variables from the CHELSA climate database (Karger et al., 2018): mean annual temperature, mean annual precipitation, and precipitation seasonality, which is the intra-annual precipitation variation, quantified as the standard deviation of the monthly estimates of precipitation from the annual mean. Annual temperature and precipitation exhibited a strong negative correlation (Fig. S1a). To derive a single composite variable of climate gradient of mean annual precipitation and temperate, we first centered the temperature and precipitation using the `*scale*` function in R version 4.2.2 (R Core Team, 2022) and then performed a principal component analysis (PCA) using the ‘*prcomp*’ function. The first principal component explained 98% of the variance and correlated positively with increasing precipitation and decreasing temperature, representing a gradient ranging from hot and dry to cold and wet climatic conditions (Fig. S9). This first principal component was used as a single variable representing climate gradient of mean annual precipitation and temperate in our analysis (hereafter, climate gradient).

**2.3 Biodiversity measures**

We assessed plant diversity at two spatial scales: **α-**scale at 10 m2 plots (n=348) and **γ-**scale at 100 m2 plots (n=174). Plant diversity was assessed for the entire plant community, including vascular plants, terricolous bryophytes and lichens. We use the terms **α** and **γ** without making any assumptions about their relationship with local or regional coexistence mechanisms. At each scale, we calculated species richness, representing the number of plant species recorded. Additionally, we calculated ENSPIE, an index of species number that explicitly accounts for the fact that rare species have a disproportionate effect on measure of species richness (Chase & Knight, 2013), because species richness weights rare and common species equally. The ENSPIE measure considers rare species as only a fraction of an ‘effective’ species and thus more heavily weights common species. ENSPIE is the *Effective Number of Species* (ENS) calculated from Hurlbert's PIE ─ *Probability of Interspecific Encounter* (Hurlbert, 1971):

where *S* is the number of species and is the proportion of the community represented by species *i* (Chase & Knight, 2013; Jost, 2006). In our analysis, the proportion of each plant species () was represented by its cover relative to the cumulative cover of plant community. ENSPIE has the same units as species richness. In a perfectly even community ENSPIE equals the species richness, but as community evenness decreases, ENSPIE becomes increasingly smaller than richness (Chase & Knight, 2013). A significant effect of an ecological driver on ENSPIE indicates that this driver altered the species abundance distributions, e.g. the distribution of commonness and rarity of species in the community. By contrasting the results of species richness and ENSPIE, we can disentangle whether the changes in biodiversity are driven by the responses of only rare species or both rare and common species. A high difference between richness and ENSPIE results suggests a strong influence of rare species on the observed response, while a low difference implies an influence of both rare and common species (Ladouceur et al., 2023).

**2.4 Data analysis**

All analyses were carried out in R version 4.2.2 (R Core Team, 2022). To test the drivers of plant diversity across scales we applied linear (LMM) or generalised linear mixed effect models (GLMM), depending on the nature of the response variables. Specifically, for the analysis of alpha species richness we applied a GLMM with the Poisson family, using the ‘*glmer*’ function of the ‘*lme4*’ package (Bates et al., 2015). For the analysis of gamma species richness we first applied a GLMM with the Poisson family, but due to overdispersion, we applied the negative binomial family using the ‘*glmer.nb*’ function from the ‘*lme4*’ package. For the analysis of beta species richness and for the ENSPIE at all spatial scales (i.e., alpha, gamma, beta) we applied LMM using the ‘*lmer*’ function from the ‘*lme4*’ package. The ENSPIE measures for all scales were log transformed to meet the assumptions of homoscedasticity. Plot ID nested in the dataset ID were used as random effects in all models for the alpha scale, and the dataset was used as a random effect in gamma and beta models. We tested random effects in all models and found them to be statistically significant and explaining substantial amounts of data variance. For an overview of the datasets used in this study see Table S1.

We used a two-step approach to test the effects of plant diversity drivers. The first model included the following predictors: climate gradient, soil organic carbon, soil pH, litter cover, grazing intensity and mowing. After inspecting the data, a quadratic term was allocated to climate gradient, soil organic carbon, soil pH and litter cover to properly model nonlinear responses. Thus, we developed a set of a priori models that allowed for unimodal effects of these predictors in all possible combinations (with and without unimodal effects) and tested if the quadratic terms impacted the predictive ability of the model. For this we used the Akaike information criterion (AIC) approach to select the most parsimonious model within the 2 units of AIC of the model with the lowest AIC. Precipitation variability was not included in the first model to avoid risk of losing signal in the climate gradient effect on biodiversity due to the co-variation of precipitation variability with the climate gradient (Fig. S1b). Specifically, precipitation variability had the hump-shaped relationship with climate gradient (Fig. S1b), indicating high precipitation seasonality in warm and moderately wet habitats in the middle of the climate gradient (i.e., in mesic and fringe grasslands) and low precipitation variability in dry and hot conditions (i.e., saline, dry and complex grassland types) and in cold and humid habitats (i.e., alpine grasslands). The effects of precipitation variability were examined separately in the second model, where all predictors (including climate gradient) were fitted as covariates. AIC was again used to evaluate the unimodal effects of precipitation variability.

**2.5 Scale-dependency of the effects of biodiversity drivers**

We evaluated the relative importance of the study predictors as drivers of plant diversity at each sampling scale by comparing their standardized effect sizes (Fig. 3a). For this, for each predictor ***x*** with a unimodal effect in the final (G)LMM model, we created the composite variable arising from the combined effects of both unsquared and squared terms of that predictor (***x*** and ***x***2). For this, the parameter estimates of ***x*** and ***x***2 were used as the loadings (weights) for the composite variable, where ***x*** and ***x***2 are multiplied by their loading and summed to generate the factor scores for the composite variable: b1×***x*** + b2×***x***2. The final (G)LMM was then refitted with the unimodal effect replaced with the composite variable. The parameter estimate of this composite variable serves as the combined effect of both the linear and non-linear effects of the target predictor ***x***. For details on the methods of using statistical composites for summarizing the collective nonlinear effects see (Grace & Bollen, 2008; J. Lefcheck, 2021). To be able to interpret and compare the parameter estimates on a comparable scale we have standardized the obtained estimate coefficients using the ‘*coefs*’ function from the ‘*piecewiseSEM*’ package in R (J. S. Lefcheck, 2016). In addition to the standardized effects, we also compared the relative variance explained by each driver on each sampling scale (Fig. 3c) by calculating partial-R2 from the (G)LMMs using the ‘*r2beta*’ function from the ‘*r2glmm*’ package in R (Jaeger, 2017).

To assess whether the influence of a given driver on plant diversity depends on the spatial scale at which diversity was measured (**α-** vs **γ-**scales) we tested the effects of the drivers on a multiplicative **β**-diversity metric (Whittaker, 1972), e.g. Fig. 2c-d:

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whererepresents the scaling factor among the two grain sizes, i.e. the spatial difference in biodiversity (species richness or ENSPIE) between **α** and **γ** scales in plot *i*, where is the biodiversity at the gamma scale (100 m2) of plot *i*, and isthe mean biodiversity of the two **α**-scale subplots (10 m2) nested within the **γ**-plot *i*.

**2.6 Underlying mechanisms of the effects of biodiversity drivers**

We evaluated the possible mechanisms underlying the effects of the drivers on local diversity (at the **α-** and **γ-**scales) and on their scale-dependency (i.e., on **β-**diversity) and summarized our findings in Fig. 4. The driver of **α-** or **γ-** diversity operated via the responses of rare species when there was a marked difference in results for species richness from the results for ENSPIE (Fig. 2). Low difference in these results implied significant contributions from the responses of the entire community, including both common and rare species (Fig. 2). For more details see the “Biodiversity measures” section above. Total plant cover affected **α-**, **γ-**,and **β-**diversity in our study (Fig. S4) and thus could mediate the effects of biodiversity drivers. When the effect of a driver on total plant cover deviated from zero (Fig. S8), the effects of this driver on the respective biodiversity measure (i.e., **α-**, **γ-**,or **β-**diversity) was assumed to be mediated by the altered total cover (Fig. 4a-b). Furthermore, when the effect size on ENSPIE at the largest sampling scale (i.e., on ) deviated from zero, the ecological driver altered the species evenness and thus affected **β-**diversity via changes in species relative cover (Chase & Knight, 2013). A significant effect of an ecological driver on indicates that the altered intraspecific aggregation in the community may mediate the different effects of this driver at different grain sizes (Chase & Knight, 2013). Increased intraspecific aggregation leads to lower diversity at a smaller scale (due to clustering of conspecifics in space), but relatively higher diversity at a larger scale, where the encountering of the aggregated species is not limited by space. Therefore, when the effect of a driver on ENSPIE changed with sampling grain (i.e., the effect on was significant, Fig. 2), the biodiversity driver was assumed to alter the intraspecific aggregation of the community.

**3. Results**

Overall, we found 1560 plant taxa (species, subspecies and aggregates) across all the study plots, out of which 1233 species of vascular plants, 171 species of bryophytes and 156 species of lichens. Plant species richness increased with the sampled scale (Fig. S3, Fig. 1b), but the difference among scales depended on the grassland habitat type (Fig. 1b).

***Effects of climate***

Both species richness and ENSPIE at **α-** and **γ-**scales showed hump-shaped responses to the climate gradient PC (Fig. 2a-b). The effects on were also hump-shaped but marginally significant, while showed no significant responses (Fig. 2c-d). Increased intraannual variation in precipitation led to higher species richness and ENSPIE measures on both scales (Fig. 1e-f), with a hump-shaped effect on but no significant effects on (Fig. 1g-h).

***Effects of soil properties***

At both **α**- and **γ**-scales, species richness had a hump-shaped relationship with soil humus (Fig. 2i) and soil pH (Fig. 2m), but these effects were more pronounced at the **γ**-scale than the **α**-scale (Fig. 3a-b). However, none of the studied soil properties significantly influenced or (Fig. 2j, Fig. 2n). While soil humus content showed no significant effect on , we observed a U-shaped effect on (Fig. 2k-l). Instead, we found a strong U-shaped effect of soil pH on but no effects on (Fig. 2o-p).

***Effects of litter cover***

Cover of plant litter had hump-shaped effects for both species richness and ENSPIE at the **α**- and **γ**-scales, with ENSPIE showing notably weaker responses compared to species richness (Fig. 2q-r, Fig. 3b). Furthermore, the relative importance of litter cover in predicting plant diversity was higher at the **γ**-scale than at the **α**-scale (Fig. 3a-b). The measures of **β**-diversity had distinct responses to litter cover: while species richness increased with litter cover, ENSPIE showed hump-shaped response (Fig. 2s-t).

***Effects of land use***

We detected no significant effects of mowing on any biodiversity measures across the studied spatial scales (Table S2, Table S3, Fig. S6). Similarly, grazing intensity did not significantly affect species richness across **α**- or **γ**-scales (Table S2, Table S3, Fig. 2u). However, contrary to species richness, there was a declining trend in with grazing intensity, although the effect was only marginally significant (Table S2, Table S3, Fig. 2v).

***Total plant cover***

We found a hump-shaped relationship between total plant cover and both **α**- and **γ**-species richness and a U-shaped relationship with (Fig. S4). Soil humus content, soil pH and litter cover had curvilinear effects of the total cover of the plant community (Fig. S8e-j), although the effects of litter cover were relatively weak, especially on the **γ**-scale (Fig. S8j).

**4. Discussion**

Spatially explicit fine-grain studies conducted at a large spatial extent are rare in macroecology (e.g., DeMalach et al. 2019, Dembicz et al. 2021a). We sampled grasslands of different habitat types across Ukraine and examined the effects of environmental drivers on plant diversity in a spatially explicit context by partitioning local diversity into two different grain sizes (**α**- and **γ**-diversity) and by examining the scale-dependency of diversity drivers by testing their effects on the scaling factor between these two scales (**β-**diversity). We explored both plant species richness and community evenness (measured by effective species richness), enabling us to uncover the mechanisms driving environment-diversity relationships and their scale-dependency (Fig. 4).

**4.1 Drivers of local plant diversity (α and γ scales)**

The climate gradient of mean annual precipitation and temperate was among the most important drivers of plant diversity at both spatial scales (i.e., **α** and **γ** plots Fig. 3). The hump-shaped effects of climate on plant diversity (Fig. 2a) can be attributed to climatic stress, where the co-occurrences of species are limited by harsh environmental conditions on the low and high ends of the gradient, such as cold areas on the high end and hot areas with drought and associated lack of snow cover during winter on the low end of the climate gradient (Fig. S1a). The peak in plant diversity in the middle of the gradient may also be linked to high site productivity due to warm and moderately wet conditions. Water availability can control primary productivity in grasslands to the extent comparable to nutrient availability, especially in dry grassland habitats (Knapp et al., 2001). The effect of climate gradient on plant diversity in our study was strongly driven by the intra-annual variability in precipitation, which, in turn, had a hump-shaped relationship with the climate gradient (Fig. S1b). Biodiversity at both study scales increased proportionally to the precipitation variability (Fig. 2e), likely because the wider range and variation in intra-annual precipitation allowed for greater niche space with larger ecological trait differences between species, and thus more species with suitable niches (Stein et al., 2014). Previous research showed that precipitation seasonality had stronger effects on plant diversity than mean annual precipitation (Towers et al., 2023), highlighting the importance of precipitation variability for the spatial distribution of plant species.

Further, we tested the effects of soil properties (when statistically controlling for climate impact) and found hump-shaped effects of both soil humus content and soil pH on species richness at both spatial scales (Fig. 2i, Fig. 2m), with soil humus showing relatively stronger effects (Fig. 3). Our results are consistent with previous studies that found soil organic carbon as a strong driver of species richness at fine spatial scales (Polyakova et al., 2016; Turtureanu et al., 2014). The hump-shaped effects of soil humus on species richness may be attributed to site productivity effects, as in most cases the soil humus content in grasslands is a measure of soil fertility and water retention, and thus can be considered as proxy for aboveground productivity. According to the *more individuals hypothesis*, higher resource availability allows species to maintain larger populations in a given area, buffering these species against extinction, and thus leading to higher species richness in more productive sites (Srivastava & Lawton, 1998). However, as plant cover increases with soil fertility (Fig. S8e-f), i.e. due to the larger population sizes and/or larger body size of individuals, the asymmetric competition among species due to space limitation causes species loss (Storch et al., 2018). In our study, the relationship between species richness and cover followed a hump-shaped pattern, thus supporting the *more individuals hypothesis* until the point where the high plant cover led to a reduction in species number (Fig. S4a-b), suggesting the asymmetric competition at the high end of the plant cover gradient.

The hump-shaped effect of soil pH on species richness can be related to the stress gradient, where the uptake of nutrients by plants is limited at low and high levels of soil pH and with toxicity at low soil pH due to exchangeable aluminium in acidic soils (Chytrý et al., 2007; Tyler, 2003). It is important to note that the highest pH values in our study were found in saline grasslands and in the dry and hot grassland habitats containing the driest soils with pronounced summer droughts and winter frosts (Fig. S2a). Despite statistical adjustments for the climate gradient in assessing soil pH effects (see “Materials and methods”), it remains challenging to disentangle the physiological effects of climatic stress (Chytrý et al., 2007; Palpurina et al., 2017) and soil salinity (Deák et al., 2014; Polyakova et al., 2016) using observational data.

Litter cover in grasslands is generally linked to the productivity–diversity relationship, as litter production is a function of annual net primary productivity in grasslands (Grime, 1979). While litter cover correlated only weakly with the site productivity proxies in our study (i.e., soil humus content and climate gradient, Fig. S2c-d), litter amounts can have profound effects on the structure of plant communities via mechanisms beyond the productivity effects (Facelli & Pickett, 1991; Loydi et al., 2013; Ruprecht et al., 2010; Ruprecht & Szabó, 2012). This is also supported by the weak hump-shaped effects of litter cover on the total cover of the plant community in our study (Fig. S8i-j). At optimal ranges, litter cover may provide key benefits for plant communities, such as soil moisture conservation, protection for seed germination and seedlings, and nutrient release during decomposition. Excessive litter amounts may inhibit germination and establishment of plants (e.g., light grass seeds), restrict plant growth (particularly ephemeroids and bulbous plants), and contribute to issues like seed rot and fungal diseases due to excessive moisture retention and increased temperature under the thick layers of compacted or matted litter (Facelli & Pickett, 1991; Ruprecht & Szabó, 2012). Furthermore, litter acts as an abiotic disturbance to grassland plant community (Dembicz, Dengler, et al., 2021; Ruprecht et al., 2010). Thus, the observed by us hump-shaped effects of litter cover on **α**- and **γ**-species richness (Fig. 2q) can also be attributed to the intermediate disturbance hypothesis, where moderate disturbances reduce interspecific competition, thus promoting species richness, which is largely due to the increased occurrences of rare species.

Presence of mowing had minor effects on plant diversity in our study (Table S2, Fig. S6). Grazing did not alter plant species number, but it reduced the evenness of the plant community (specifically at , Fig. 2v), indicating that some species became more dominant with increasing grazing intensity, likely these were the grazing-tolerant species favoured by grazing (Buzhdygan et al., 2020). Numerous evidence points toward land use as a major driver of local plant diversity in grasslands (Petermann & Buzhdygan, 2021; Sala et al., 2000). The low explanatory power of land use in our study may be attributed to the fact that our study plots were deliberately selected to avoid high-intensity management. This is because the main focus of our study is on the natural biodiversity drivers across different grassland habitat types. Furthermore, the rates of land-use abandonment in Ukrainian grasslands, as well as across Europe, have increased in recent years (Buzhdygan, Tietjen, et al., 2020; Enyedi et al., 2008; Petermann & Buzhdygan, 2021), leading to a rather short gradient of land use intensity in our study. Nearly 48% of our study plots belong to zonal (natural) vegetation (Fig. S7), which, unlike seminatural grasslands, are maintained by natural abiotic and biotic processes and do not require human interventions in natural conditions (Török et al., 2018).

Numerous studies in grasslands have identified soil properties, such as humus content and pH, as the most important drivers of the fine-scale species richness (Chytrý et al., 2003, 2007; Dembicz, Velev, et al., 2021; Schuster & Diekmann, 2003), while other studies found no effect (Kuzemko et al., 2016; Turtureanu et al., 2014). In our study the effects of the broad-scale climatic variables prevailed over those of the local effects of soil properties and of litter cover (Fig. 3). The correlation of soil characteristics and litter cover with the climate gradient and grassland habitat type (Fig. S2) partially explains these results, similarly to those shown in previous studies, e.g. for soil properties in (Palpurina et al., 2017) and for litter cover in (Dembicz, Velev, et al., 2021).

**4.2 Mechanisms underlying the drivers of local plant diversity (α and γ scales)**

Using species richness as sole proxy of biodiversity across different grassland habitat types can strongly overestimate the detection of the inherent ecological differences among the studied plant communities, because the responses of species richness metrics to ecological drivers depend critically on the size of the species pool (Chase & Knight, 2013). In our study we used the ENSPIE measure, because it is independent of species pool (Chase & Knight, 2013) and the comparison of the responses of ENSPIE to ecological driver to those of species richness allows elucidating whether the observed effect of this driver on biodiversity is driven by the responses of locally rare or common (abundant) species (Blowes et al., 2022; Chase & Knight, 2013; Ladouceur et al., 2023).

Previous research in grasslands suggests that the relationship between precipitation and species richness is mediated by species pool rather than by local interspecific competition (Adler & Levine, 2007; Foster & Dickson, 2004). In our study, however, the effects of climate variables affected both species richness and ENSPIE (similar shape and strengths of the effects, Fig. 2a-b), indicating that climate not only altered species occurrences but also species abundance distributions, and that the climate-biodiversity relationships were strongly affected by the responses of common species. Specifically, in the middle of the climate gradient, plant communities were not only the species richest, but also had more even relative abundances (i.e. higher ENSPIE, Fig. 2a-b). This could be attributed to the facilitative coexistence of stress-tolerant species with competitive stress-intolerant species at intermediate levels of environmental stress (Michalet et al., 2006).

In contrast to climate, the hump-shaped effects of soil humus content and soil pH on plant diversity (Fig. 2i, Fig. 2m) were determined rather by the responses of rare species, as we found no significant effects of these variables on ENSPIE (Fig. 2j, Fig. 2n). High soil productivity (e.g., with increasing soil humus in our study grassland plots) generally leads to asymmetric competition among plant species, resulting in lower population densities of initially rare species and their subsequent extinctions (Rajaniemi, 2003). However, in severe environmental conditions, such as low and high soil pH, biotic interactions become less important than environmental stress, and only stress-tolerant species can persist (Michalet et al., 2006). Both acidification and high alkalinity of soil limit the plant species pool to pH-tolerant specialists (Schuster & Diekmann, 2003). Furthermore, temperate regions have smaller species pools for highly productive habitats since these habitats have been rare in evolutionary history (Pärtel et al., 2007). Similarly, the evolutionary species pool of vegetation in the majority of temperate Eurasian habitats evolved from historically prevalent neutral to slightly high soil pH (Chytrý et al., 2007; Ewald, 2003; Pärtel, 2002). This suggests that evolutionary species-pool effects could also contribute to the low species richness at the high end of the soil humus gradient and at low soil pH levels, as found in our study (Fig. 2i, Fig. 2m).

The effects of litter cover on species richness were determined by the responses of both locally common and rare species, with rare species playing an important role, as indicated by relatively weaker effects on ENSPIE than on species richness (Fig. 2q-r, Fig. 3). Moderate amounts of litter can reduce species competition for light resources by physically separating plants and reducing light availability to dominant competitive species (Facelli & Pickett, 1991; Lamb, 2008). This creates opportunities for less competitive and locally rare species to establish. Similarly, the litter patches foster microscale variations in nutrient availability, promoting niche differentiation and coexistence of diverse plant species.

Overall, our results suggest that the underlying mechanisms of the environment-biodiversity relationship strongly depend on the ecological driver (Fig. 5a). The effects of climate on grassland plant diversity are a complex interplay between environmental stress and site productivity effects. High productivity and low climatic stress shifted species abundance distributions, likely through altered species interactions (e.g., competition, facilitation). In addition to productivity effects, high intra-annual precipitation, in the middle of the climate gradient, affected plant diversity likely by promoting niche differentiation. The effects of high stress conditions of climate (i.e., cold and drought) and of soil (low and extremely high soil pH) on plant diversity likely operated by filtering non-competitive but stress-tolerant species. Soil fertility increased plant diversity, likely by supporting more viable populations of species (*more individuals hypothesis*) until the high end of the soil productivity gradient, where increased asymmetric competition due to high plant cover (Fig. S8e-f) likely caused species extinctions. Additionally, the effects of the evolutionary species pool may have limited plant diversity at both high soil fertility and low soil pH levels. Moderate biotic disturbance, caused by litter cover, promoted plant diversity likely due to the patchiness of resources and reduced asymmetric competition of dominant competitive species.

**4.3 Scale-dependency of plant diversity and of diversity-environment relationships**

Our results agree with the general notion that plant species richness depends on sample grain (Fig. S3a) (Field et al., 2009; Siefert et al., 2012), and that the scale-dependency of diversity varies with grassland habitat (Fig. 1b). Additionally, the overall explanatory power for species richness by our set of ecological drivers was weaker at smaller grain size (Fig. S3c). This is in line with previous studies (Bergauer et al., 2022; Filibeck et al., 2019; Kuzemko et al., 2016; Talebi et al., 2021) and is likely attributed to the fact that towards finer grains stochastic processes become more important for species co-occurrences, and thus diversity becomes more variable and less predictable by environmental factors (Barton et al., 2013).

Comparing how the effect sizes of ecological drivers on species richness vary with sampling grain (i.e., **α-** vs **γ-**scale, Fig. 4) allows estimating the relative importance of the driver in governing plant diversity depending on spatial scale. In our study, the strength of effects for most of the indicated drivers differed between the two study grain sizes (Fig. 3), but neither the shape nor the direction of these effects changed with scale (Fig. 2). In contrast to large-scale studies, such as comparing plot vs site or regional scales (Chase & Leibold, 2002; Šímová et al., 2013), previous fine-scale studies in grasslands have repeatedly shown that the shape and direction of effects for most of the drivers are robust to sampling grain (Dembicz, Dengler, et al., 2021; Dembicz, Velev, et al., 2021; Polyakova et al., 2016; Turtureanu et al., 2014), but for contradicting results see (Bergauer et al., 2022; Kuzemko et al., 2016). Indeed, the majority of previous fine-scale research in grasslands has mainly focused on the primacy (primary influence) and the relative importance of biodiversity drivers across grain sizes and extent (Auestad et al., 2008; Bergauer et al., 2022; Dembicz, Velev, et al., 2021; Kuzemko et al., 2016; Olagoke et al., 2023; Polyakova et al., 2016; Talebi et al., 2021; Turtureanu et al., 2014), while the underlying mechanisms of such scale-dependency were rarely tested (DeMalach et al., 2019). The theoretical models for decoupling these mechanisms (Chase & Knight, 2013; Storch et al., 2018) show that changes in total community cover, relative cover (evenness), and intraspecific aggregation are major mediators of the scale-dependency of biodiversity driver effects in different ecosystems, including grasslands (DeMalach et al., 2019; Dembicz, Dengler, et al., 2021). The shape and strength of the driver effect on the relationship of ENSPIE with the sample scale (e.g., on, Fig. 2) provide information on whether the scale-dependency of the driver effects may operate via the altered abundance distribution of species and intraspecific aggregation (Chase & Knight, 2013). Intraspecific aggregation plays an important role in the scale-dependency of biodiversity if the community at a smaller scale is more uneven (i.e., lower ENSPIE values) than at a larger scale (Chase & Knight, 2013).

In our study, the hump shape of the climate ─ richness relationship was robust to sampling grain size (Fig. 2a-b), and the effect of climate gradient on was not significant (Fig. 2c). Instead, the hump-shaped effect on indicates a larger difference in community evenness among **α**- and **γ**-scales towards the middle of the climate gradient (Fig. 2d), suggesting higher species aggregation in more productive sites. These findings align with previous empirical studies that have suggested a positive correlation between productivity and intraspecific aggregation, resulting in larger effects of productivity on richness at larger spatial scales compared to smaller scales (Chalcraft et al., 2008; Chase & Leibold, 2002). Our results regarding soil productivity also support these findings, as we found an increase in at high soil humus content (Fig. 2l), also suggesting higher intraspecific aggregation with increasing site productivity. Precipitation variability showed a significant curvilinear negative effect on (Fig. 2g), indicating higher differences in richness among scales in habitats with intermediate precipitation variability (e.g., alpine habitats) and decreased difference towards the high end of the axis (e.g., mesic grasslands – also among the most species rich habitats in our study, Fig. 1b). Previous research on plant richness across a wide gradient of grassland habitat types concluded that the effects of macroclimatic gradients on fine-grain species diversity do not depend on grain size (Dembicz, Dengler, et al., 2021). While our results partially agree with this finding, they also suggest that using species richness as the sole proxy for biodiversity may underestimate the scale-dependency of climate and soil effects across different grassland habitat types, due to difference in the species pool. Indeed, grassland studies within more climatically uniform regions or habitat types showed more pronounced climate effects on the richness ─ scale relationships (-diversity), such as in perennial sand grasslands in Hungary (Bartha et al., 2011), Iranian steppes (Talebi et al., 2021), semi-desert areas in South Africa and Namibia (van der Merwe & van Rooyen, 2011), and across global drylands (DeMalach et al., 2019).

Not only the availability of resources (site productivity), but also their patchiness is known to increase the propensity for species to aggregate, which, in turn, may enable species coexistence by reducing interspecific competitive exclusion (Wassmuth et al., 2009) because the competitively weak species generally suffer less from conspecifics than from competitively strong heterospecifics (Stoll & Prati, 2001). The highest difference in from near the middle of the litter-cover gradient in our study (the concave-down effect on , Fig. 2t) also suggests intraspecific aggregation, likely due to a mosaic of microhabitats caused by moderate litter amounts, thus leading to larger effect sizes on community evenness at larger relative to smaller spatial scales (Fig. 3). Furthermore, we found a linear increase in with litter cover (Fig. 2s), indicating higher among-scale difference in species number but not in evenness at the high end of the litter gradient. Such spatial differences were likely constrained by the limited space of the smaller grain, as the litter effects on richness were strong at the **γ** scale but relatively weak at the **α** scale (Fig. 2q). Overall, our results suggest that the occurrences of species at high disturbance (as caused by excessive litter) were constrained by the space limitation, likely due to higher chances of including more microhabitat patches with increasing area, and thus more species that can occupy these patches (Tamme et al., 2010). Our results also agree with studies of the Romanian dry grasslands (Turtureanu et al., 2014) and the Ukrainian steppes (Kuzemko et al., 2016), which found an increase in the relative influence of litter cover on plant species richness with increasing grain size. Furthermore, in our study, litter cover was among the most important drivers of and(Fig. 3b), which also agrees with the previous studies of fine-scale species-area relationship in grasslands (Turtureanu et al., 2014).

Space limitation also played an important role in the scale-dependency of plant diversity responses to soil stress. Specifically, the overall effects of soil pH on species richness were significantly weaker at the **α** scale than those at the **γ**-scale plots (Fig. 3, Fig. 4), but with a strong U-shaped pattern of the effect on , while no effect on(Fig. 2o-p). This indicates that the occurrence of species under soil-related stress (i.e. toward low and high soil pH) was strongly limited by the area size, which is likely driven by the loss of locally rare species (Schuster & Diekmann, 2003). Previous studies also found the U-shaped relationship between soil pH and the fine-scale **β**-diversity in grasslands (Dembicz, Dengler, et al., 2021). We found no effects of soil pH on(Fig. S2g) or on community evenness (and , Fig. 2), thus suggesting that the scale-dependency of soil-pH effects were not operating through the changes in species relative cover or in species aggregations, but were rather direct, likely due to smaller species pools in more acidic or basic sites. Our results agree with (DeMalach et al., 2019), who found that the effects of soil pH on species-area relationship across global drylands were not mediated by intraspecific aggregation or species evenness in plant communities.

Although we found no significant effects of grazing or mowing on **β**-diversity (Fig. 2x), the negative effect of grazing intensity on ENSPIE became more detectable at the **γ** scale (Fig. 2v). These results somewhat agree with previous studies suggesting that land use becomes a more important predictor of grassland plant diversity at larger scales (Auestad et al., 2008; Spiegelberger et al., 2006; Turtureanu et al., 2014). The scale-dependency of management effects on plant diversity in grasslands is shown to vary considerably along climatic gradients, e.g. as shown for grazing (de Bello et al., 2007), or management types (Dupré & Diekmann, 2001; Spiegelberger et al., 2006). Therefore, the scale-dependency of land-use effects may become more detectable in climatically more uniform grassland habitat types, for example as found for the semi-natural grasslands in Norway (Auestad et al., 2008), semi-natural dry grasslands in Romania (Turtureanu et al., 2014), step grasslands in Ukraine (Kuzemko et al., 2016), and alpine grasslands in Europe (Spiegelberger et al., 2006).

Increased area size is associated with higher energy availability on the site (Šímová et al., 2013). Thus the *more individuals hypothesis* (MIH) has been regarded as the main explanation of the nested species-area relationship (Gaston, 2000), which advocates that spatial variation in species richness is mediated by the environmentally and spatially dependent variation in the number of individuals of a species. Our results, however, showed a relatively weak relationship between total plant cover and **β**-diversity (Fig. S4c), suggesting that MIH is not necessarily the most important mechanism underlying the scale-dependency of plant diversity at fine spatial scales. However, the caveat of using plant cover as the proxy for plant abundance is that plant cover may increase not only with the number of plant individuals but also with their body size. The U-shape of the relationship between plant cover and **β**-diversity (Fig. S4c) indicated that the scale-dependency of plant diversity decreased with plant cover until the higher end of the cover gradient where the excessive cover of the plant community reduced richness, likely due to asymmetric competition among species. Among the studied biodiversity drivers, only soil humus content and soil pH had significant curvilinear effects on plant cover. Additionally, the effect of litter on plant community cover was curvilinear but weak (Fig. Si-j). Overall, our results suggest that in addition to the mechanisms discussed above, altered plant cover could partially mediate the scale-dependency of the effects of soil humus, soil pH, and litter cover on plant diversity (Fig. 5).

By identifying key drivers and their scale-dependent effects on plant diversity, our results underline the need for integrated and adaptive conservation strategies tailored to different spatial scales and grassland habitat types and call for management approaches that account for the complex interactions between biodiversity drivers and spatial scales in grassland ecosystems. Understanding the mechanisms underlying these scale-dependent effects enhances our ability to predict and mitigate the impacts of environmental changes on grassland biodiversity and have important application for management and conservation, as species-area relationship is often used for biodiversity assessment for conservation and management applications (e.g., Smith 2010, van der Merwe and van Rooyen 2011, DeMalach et al. 2019).

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**Data availability**

Upon acceptance data required to reproduce the analysis in this study will be submitted into a repository with a doi link and will be available open access.

**Code availability**

The codes for the analyses of this study are available at <https://github.com/oksanabuzh/Buzhdygan_et_al_sCale_Div_Driver>. Upon acceptance the final repository of the code will be also submitted into a repository with a doi link.

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**Conflict of Interests**

The authors declare no conflict of interests.

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