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Functional traits trade-offs define plant population stability across different biomes.

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Functional traits trade-offs define plant population stability across different biomes

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The following **supplementary material** is available in a separate file (Conti et al. Supplementary material.pdf):

Fig. S1 Effects of continuous traits on detrended mean species variability (CVt3).

Fig. S2 Effects of continuous traits on the two components of species variability (CV): mean abundance and standard deviation.

Fig. S3 Relationships across datasets: random slope effects in single trait models.

Fig. S4 Effects of life span and continuous traits on species variability (CV).

Fig. S5 Trait influence on species variability beyond and in addition to phylogenetic relatedness.

Table. S1 Effects of PCoA axes and single traits on mean species variability (CV).

Table S2 Dataset information (Separate file: "Table S2 Datasets information.xlsx")

Table S3 Functional traits information (Separate file: "Table S3 Traits information.xlsx")

1 **Abstract**

2

3 Ecological theory posits that temporal stability patterns in plant populations are associated with
4 differences in species' ecological strategies. However, empirical evidence is lacking about which
5 traits, or trade-offs, underlie species stability, especially across different biomes. We compiled a
6 worldwide collection of long-term permanent vegetation records (>7000 plots from 78 datasets)
7 from a large range of habitats which we combined with existing trait databases. We tested whether
8 the observed inter-annual variability in species abundance (coefficient of variation) was related to
9 multiple individual traits. We found that populations with greater leaf dry matter content and seed
10 mass were more stable over time. Despite the variability explained by these traits being relatively
11 low, their effect was consistent across different datasets. Other traits played a significant, albeit
12 weaker, role in species stability, and the inclusion of multivariate axes or phylogeny did not
13 substantially modify nor improve predictions. These results provide empirical evidence and
14 highlight the relevance of specific ecological trade-offs, i.e. in different resource use and dispersal
15 strategies, for plant populations stability across multiple biomes. Further research is however
16 necessary to integrate and evaluate the role of other specific traits, often not available in databases,
17 and intraspecific trait variability in modulating species stability.

18

19

20 **Keywords:** acquisitive; conservative; dispersal; worldwide database; long-term studies; resource
21 use; temporal patterns; variability

22

23

24

25 **Introduction**

26 Identifying the drivers of temporal stability in plant populations and communities has consequences
27 for maintenance of multiple ecosystem functions over time, including carbon sequestration, fodder
28 resources for livestock, and nutrient cycling (Tilman & Downing, 1994; Hautier *et al.*, 2015; Isbell *et*
29 *al.*, 2018). One of the main determinants of community stability is the cumulative temporal
30 variability in the abundances of individual species' populations (Thibaut & Connolly, 2013; Hallett *et*
31 *al.*, 2014; Májeková *et al.*, 2014). Lower temporal variability in individual population abundances at
32 a given site, and particularly for dominant species, generally increases overall community stability
33 (Lepš *et al.*, 1982, 2018; Pimm, 1984; McCann, 2000). Accordingly, assessing the drivers of temporal
34 variability in populations is necessary to understand and forecast the potential consequences of
35 increasingly common environmental perturbations (Easterling *et al.*, 2000; Lloret *et al.*, 2012).

36 While empirical evidence is still scarce and ambiguous, theoretical predictions suggest that
37 the drivers of temporal variability in single plant populations are related to different ecological
38 characteristics of species (e.g., r/K life history strategies, MacArthur & Wilson, 1967). These
39 differences can be described through functional traits that determine how plants respond to
40 environmental factors, affect other trophic levels, and influence ecosystem properties (Lavorel &
41 Garnier, 2002; Kattge *et al.*, 2011; Garnier *et al.*, 2016). Specifically, differences in functional traits
42 among species result in varied responses to the environment that might lead to different patterns
43 of demography, adaptation, and distribution, thus giving rise to different population fluctuations
44 over time (e.g. Angert *et al.*, 2009; Metz *et al.*, 2010; Adler *et al.*, 2013; Májeková *et al.*, 2014).

45 Assessing differences in functional traits between species, as well as the relationship of these
46 differences to specific ecological patterns, has been a long-standing focus in plant ecology leading
47 to a search for general trait trade-offs across taxa and ecosystems (e.g. Díaz *et al.*, 2016). Trait trade-
48 offs are generally understood as a shift in the balance of resource allocation to maximize fitness
49 within the constraints of finite resources (e.g. Grime's C-S-R strategy scheme; Grime, 1977). Mostly,
50 such trade-offs have been assessed within the context of community assembly theory and eco-
51 evolutionary models for niche differentiation (e.g. Villa-Martin *et al.*, 2016; Falster *et al.*, 2016;
52 Mayfield *et al.*, 2010). Ultimately, traits linked to specific axes of ecological differentiation are key
53 to understanding major trade-offs in plant strategies, such as the trade-off between leaf maximum
54 photosynthetic rate and leaf longevity, also known as the leaf economic spectrum (Wright *et al.*,
55 2004).

56 At the same time, different specific trade-offs can also underlie differences in temporal
57 variations in species' abundances, both within and between community types. For example, species
58 that are able to respond quickly to environmental variability, i.e. acquisitive resource-use strategy,
59 fast-growing species that invest in organs for rapid resource acquisition and/or high dispersal ability,
60 should sustain higher temporal variation in population size, and will be favoured in sites where
61 disturbance and/or environmental instability determine a fluctuation in resources (MacArthur &
62 Wilson, 1967; Westoby, 1998; de Bello et al. 2021). In contrast, species adapted to endure
63 environmental variability, i.e. conservative resource-use strategy, slow-growing and long-lived
64 species that invest in structural tissues and permanence, are thought to persist during unfavourable
65 periods due to resources stored from previous, more favourable years (Reich, 2014), and will exhibit
66 less temporal variability (MacArthur & Wilson, 1967; Grime, 2001). These species are expected to
67 be favoured in more stable and predictable environments (Kraft *et al.*, 2014).

68 It remains unclear though whether the potential relationship between species' traits and
69 species' stability would be detected across different biomes and through differences in single traits
70 or combined axes of differentiation that incorporate multiple traits (Westoby, 1998; Laughlin, 2014;
71 Díaz, *et al.* 2016). Several ecological strategy schemes, such as the classic r/K selection (MacArthur
72 & Wilson, 1967) and C-S-R (Grime, 1977) theories, as well as the Leaf-Height-Seed scheme ('LHS';
73 Westoby, 1998), can theoretically help predict how functional trade-offs determine species'
74 temporal strategies and their fitness across different types of environments. The LHS scheme for
75 instance, is based on three independent plant traits which should provide key proxies for
76 independent trade-offs in plants (stress adaptation, competition, and response to disturbance
77 respectively; Westoby, 1998). Interestingly, only a few empirical studies have linked differences in
78 temporal strategies to functional traits within plant communities (Adler *et al.*, 2006; Angert *et al.*,
79 2009; Metz *et al.*, 2010; Májeková *et al.* 2014; Craven *et al.*, 2018). For example, Májeková *et al.*
80 (2014) empirically confirmed that herbaceous species with a more conservative resource-use
81 strategy (i.e., those with higher leaf dry matter content – LDMC) have more stable populations over
82 time. A similar relationship was found at the community level, where communities including a
83 greater abundance of species with high LDMC were more stable (Polley *et al.*, 2013; Chollet *et al.*,
84 2014). A recent global meta-analysis of sown grasslands, although based on short-term experiments,
85 suggested that an increase in the abundance of rapidly growing species can destabilize community
86 biomass over time (Craven *et al.*, 2018). This is supported by empirical demonstrations that, in
87 natural vegetation, community stability is predicted by the functional traits of the dominant species

88 rather than by species diversity *per se* (Lepš *et al.*, 1982). Further, only Májeková *et al.* (2014) tested
89 whether trait-based predictions of population temporal variability were consistent across different
90 management regimes, i.e. fertilization and competitor-removal treatments, generally finding minor
91 differences and consistent predictions for LDMC. Ultimately, global empirical evidence of a general
92 link between quantitative functional traits and the temporal variability of populations, and whether
93 this link is maintained despite differences in community types and environmental conditions, is still
94 missing (de Bello *et al.*, 2021).

95 Here, using an extended compilation of long-term, recurrently monitored vegetation plots,
96 encompassing different habitat types around the World (<https://lotvs.csic.es/>; Sperandii *et al.*,
97 2022) we determine which plant traits better predict the temporal stability of plant populations. We
98 expect that populations of species with more acquisitive and higher dispersal-ability traits will tend
99 to be more variable over time, while those of species with more conservative trait values and lower
100 dispersal ability will tend to be more stable over time. We also expect to find empirical evidence of
101 the generality of these relationships.

102

103 **Materials and Methods**

104 *Plots and population's stability*

105 We used 78 datasets contained in the LOTVS collection of temporal vegetation data. These consist
106 of a total of 7396 permanent plots of natural and semi-natural vegetation that have been
107 consistently sampled for periods of between six and 99 years, depending on the dataset
108 (supplementary material Table **S2**; Valencia *et al.* 2020a, Sperandii *et al.* 2022). These datasets were
109 collected from study sites in different biomes that span the globe, in 18 different countries including
110 Australia, China, Czech Republic, Estonia, France, Germany, Hungary, Kenya, Mongolia, Netherlands,
111 New Zealand, Norway, Russia, South Africa, Spain, Switzerland, United Kingdom and USA. They differ
112 in sampling method (e.g., abundance measured as above-ground biomass, visual species cover
113 estimates, species individual frequencies), plot size, and study duration. The studies that generated
114 the datasets sampled different types of vegetation (predominantly grasslands but also shrublands
115 and forests) and covered a wide array of biomes, with mean annual precipitation spanning from 140
116 mm to 2211 mm, highest temperature of the warmest month spanning from 11.3°C to 35.7°C, and
117 lowest temperature of the coldest month spanning from -35.3°C to 7.7°C (supplementary material
118 Table **S2**).

119 First, for each plot we quantified the inter-annual variability in the size of each species'
120 population using the coefficient of variation (CV) of abundance over time, i.e. the standard deviation
121 of species abundance over mean species abundance (Májeková *et al.*, 2014; de Bello *et al.*, 2021).
122 Since a fundamental differentiation between growing strategies corresponds to whether a species
123 is woody or non-woody (Reich, 2014; Díaz *et al.*, 2016) we focused the main analyses on non-woody
124 species only. This meant, we excluded any species belonging to forest overstories (i.e. trees and
125 shrubs), woody species' seedlings, and any other species defined as woody when present in the
126 plots. Moreover, based on the collected data available, in many plots we could not distinguish adult
127 woody individuals from seedlings, with seedlings most likely being the cause of high variability in
128 woody species' CV values (see Fig. **2a**). Nevertheless, we tested differences in CV values between
129 woody and non-woody species in our data and we considered a possible influence of the presence
130 of woody overstory on the CV values (see data analysis).

131 To avoid using biased CV values for very sporadic species (increased CV), we also excluded
132 those species that occurred in fewer than 30% of the sampling events across the time series for a
133 given plot (Májeková *et al.*, 2014). Further, to account for variability in CV values between and within
134 the datasets, mostly due to differences in abiotic, biotic, and management conditions, we calculated
135 the average CV value for each species in each dataset, standardizing and scaling these averages
136 within each dataset (z-scores). This resulted in a total of 3,397 species *per* dataset CV values. To
137 account for potential effects of temporal directional trends in vegetation affecting CV (Valencia *et al.*,
138 2020b) we also computed a detrended version of CV (CVt3) which gave very similar results to
139 the basic CV calculations (see supplementary material Fig. **S1**).

140

141 *Functional traits*

142 For all the species in our dataset, we collected trait information from the TRY global database (Kattge
143 *et al.*, 2020). We considered different functional traits representing different components of major
144 plants' growing strategies (Westoby 1998). Regarding categorical traits, we considered life span
145 (annual and non-annual); life form; woodiness (woody and non-woody), and growth form. For
146 continuous traits we analysed plant height, seed mass, specific stem density, LDMC, specific leaf
147 area (SLA), leaf nitrogen content *per* unit mass, and leaf phosphorus content *per* unit mass (see
148 Garnier *et al.*, 2017 for trait name nomenclature and definitions). Beside considering the effects of
149 these traits separately, we also evaluated the effect of both categorical traits and quantitative traits
150 together (see supplementary material Fig. **S4**) and the effect of quantitative traits beyond

151 categorical traits. Furthermore, considering phylogeny as a proxy of conserved functional traits, we
152 considered the effect of potentially unmeasured traits (see supplementary material Fig. **S5b**).

153 For each species, we averaged trait values across all standard measurements obtained from
154 TRY, excluding those performed under explicit treatments, on juveniles, and outliers. The traits that
155 were log-transformed (using natural logarithm) to achieve a normal distribution. For details on the
156 traits used, their summary statistics, their correlations, and their coverage in each dataset, see
157 supplementary material Table **S3**. To take into account multivariate trade-offs between species, we
158 also considered axes of functional variation derived from multivariate analyses (Principal
159 Coordinates Analysis, PCoA). The traits considered were weakly inter-correlated, with the two major
160 axes of trait differentiation from PCoA, linked mainly to LDMC and seed mass (see supplementary
161 material Table **S1** for details). The taxonomic names follow the nomenclature of 'The Plant List'
162 (www.theplantlist.org). Nomenclature was standardized using the R package 'Taxonstand' (Cayuela
163 *et al.*, 2017).

164

165 *Data analyses*

166 To quantify how the considered traits were linked to species CV, we used linear mixed effect models
167 ('lmer' function in R package "lme4", Bates *et al.*, 2014). As a response variable, we used the mean
168 CV for each species in each dataset, standardized as mentioned above. To analyse the effect of the
169 continuous traits, we fitted a single model. As predictors, we included all the continuous traits listed
170 above, scaled and centered. To account for the taxonomic and spatial structure of the data, we
171 included both species identity and dataset identifier as random intercept factors in all of the models.
172 We visually checked the compliance of all of the models residuals with normality and
173 homoscedasticity. To assess the goodness-of-fit of the full model, fixed (i.e. marginal) and total (i.e.
174 conditional) R^2 were calculated (Nakagawa & Schielzeth, 2013; Nakagawa *et al.*, 2017). To define
175 which among the continuous traits were more relevant for species stability, we compared the fixed
176 R^2 of different models, each differing in the subset of predictors that were included. These different
177 models were fitted to different datasets because of the presence of missing values in the trait data.
178 We used R^2 as a unifying measure of goodness of fit, i.e. as a measure of how well the different
179 models explain the variability in the different datasets. Using this approach, we selected the model
180 that had the highest fixed R^2 . In the present work, we focused on significant terms in the reduced
181 model. For completeness, we also compared AIC of full and reduced models by fitting them to the
182 same subset of the data, i.e. we fitted the reduced model to the dataset of the full model. We found

183 that the AIC was indeed lower when using a subset of the trait variables (AIC of the full model was
184 1939.2, AIC of the reduced model using the same data frame was 1934.6). Separate models were
185 fitted to clarify the influence of categorical traits on the stability of species, each using either
186 woodiness, life span, life form, or growth form as predictors. In these models, we excluded the
187 intercept, to better see the differences between the trait categories. In addition, analogous models
188 were run also on the two components determining species' CV separately, i.e. mean abundance and
189 standard deviation of abundance in time, also standardizing these variables within each dataset
190 (supplementary material Fig. **S1**).

191 A series of analogous models were fitted using a different set of predictors, all shown in the
192 supplementary material. To examine the influence of differentiation axes based on multiple traits,
193 instead of using single separate traits, models were run using two multivariate PCoA axes that
194 resulted from the combination of traits. We also fitted separate models using each single trait of
195 those emerging as significant in the reduced multivariate model (See supplementary material Table
196 **S1**). To explore the consistency of the stability-trait relationships across datasets, we also fitted
197 models using each single trait and adding a random slope effect for the datasets (supplementary
198 material Fig. **S3**). We also tested the interaction between the most influential categorical trait,
199 namely life span, and the other continuous traits (see Fig. **S4**). Finally, a set of models was fitted to
200 assess the possible effect of phylogenetic relatedness on the results found. Specifically, we tested
201 to what extent considering phylogeny modified the effect of the considered traits and whether
202 phylogeny, considered as a proxy of unmeasured traits, improved the main models emerging from
203 the analyses of quantitative traits (see supplementary material Fig. **S5** for all the details regarding
204 these models).

205

206 **Results**

207 By focusing initially on continuous traits, we were able to detect two sets of key functional traits
208 playing a consistent role in species' population temporal stability: one linked exclusively to seed
209 mass, and the other linked to the leaf economic spectrum, i.e. LDMC, SLA, and Leaf N content. Based
210 on the reduced linear mixed effect model, these two sets of traits had the most influence on species
211 CV among the continuous traits considered (Table **1**; Figure **1**).

212 We found significant negative coefficients with species CV for LDMC and for seed mass (Table
213 **1**; Fig. **1**). These coefficients indicate that species with greater LDMC and greater seed mass were
214 more stable (i.e. lower CV values; Fig. **1a**). In contrast, we found positive coefficients for SLA and

215 Leaf N content, although the effect was statistically significant only for SLA. For these traits, the
216 larger the trait value, the higher the species CV and therefore the less stable the species populations
217 (Fig. **1b,d**). The effect of these traits was reasonably consistent across datasets (low deviation of the
218 datasets' random slope effect compared to the main effect slope for both the models using LDMC
219 and seed mass; supplementary material Fig. **S3**). Since the variability explained by individual traits
220 was relatively low ($R^2=0.07$ for fixed effects in the reduced model using the quantitative traits, Table
221 1) we assessed the role of combining quantitative traits into multivariate axes, categorical traits, or
222 by considering phylogeny.

223 Similar results to individual traits were found using either of the two first PCoA axes based
224 on multiple traits (supplementary material Table **S1**), although with a slightly lower predictive power
225 (R^2 fixed was 0.05 compared to 0.07 in the reduced model that used individual traits). We also fitted
226 models using the single PCoA axis and the single traits. In this case single trait models again explained
227 more variability compared to the models with the single PCoA axis (PCoA Axis 1 model's R^2 fixed was
228 0.040 vs 0.050 when using LDMC; PCoA Axis 2 model's R^2 fixed was 0.003 vs 0.005 when using seed
229 mass; supplementary material Table. **S1**). Although we realize that these models are fitted to subsets
230 of the database having different species numbers and datasets, R^2 , as a generic measure of goodness
231 of fit, gives us an indication that the models using functional traits perform better than the ones
232 using aggregated axes of functional differentiation. Moreover, using R^2 to compare models with
233 PCoA axes and the single traits is not problematic because the models have the same number of
234 degrees of freedom. Finally, when the two components determining species' CV were analysed
235 separately, i.e. species' mean abundance and standard deviation of abundance over time, the model
236 predicting mean abundance was stronger than the model using standard deviation of abundance
237 over time (with significant results and a higher R^2 fixed; see supplementary material Fig. **S2**) although
238 LDMC predicted significantly both mean abundance and its standard deviation.

239 Categorical traits provided some improved predictions compared of using continuous traits,
240 both influencing CV alone (Table **2**) and in combination with quantitative traits (Fig. **S4**). Herbaceous
241 species with longer life span (i.e. perennial and biennial) tended to have a lower CV (fixed $R^2=0.04$;
242 Table 2). Adding life span to the models with quantitative traits, however, did improve predictions
243 only slightly (fixed R^2 increased to 0.10). Most importantly the interaction between life span and the
244 quantitative traits considered was not significant, indicating that, for example, LDMC was a good
245 predictor of stability for both non-annual and annual species. Woody species, trees and shrubs also
246 had low CV scores (although with very low fixed $R^2= 7.04e-07$). Finally, after accounting for

247 phylogeny (i.e. adding phylogenetic eigenvectors to 'correct' CV values) there was no evidence for
248 an overall improvement in model explanatory power (fixed R^2 was 0.01) nor did this substantially
249 modify the results (see supplementary material, Fig. **S5**). At the same time, the phylogenetic signal
250 not accounted for by the considered traits (decoupled phylogenetic information; de Bello et al. 2017;
251 Fig. **S5**), used here as a proxy of unmeasured traits, did not change the original explained variability
252 (fixed R^2 stayed at 0.07).

253

254 **Discussion**

255 By analysing a large worldwide compilation of permanent vegetation plot records, we confirmed
256 the generality and consistency of theoretical predictions relating key functional traits to plant
257 population stability over time. We specifically found that the species with greater LDMC and a larger
258 seed mass were the most stable over time. Ultimately, these results suggest that common functional
259 trade-offs related to resource use and dispersal consistently influence herbaceous plant population
260 stability across different biomes worldwide. While the results clearly demonstrates that simple plant
261 traits can help, consistently, in predicting the stability of individual species, and ultimately of plant
262 communities, the variability explained by these traits was relatively low, despite accounting for
263 other key traits like life span or using phylogeny as a proxy of unmeasured traits. Further research
264 is therefore necessary to integrate and evaluate the role of intraspecific trait variability and other
265 potentially relevant traits, generally not available in trait databases, in modulating species stability.

266 We identified two likely functional trade-offs that influence species stability. Specifically,
267 differences associated with the leaf economic spectrum (in our case linked to LDMC, SLA and N
268 content values) define trade-offs in terms of slow-fast resource acquisition (Wright *et al.*, 2004; Díaz
269 *et al.*, 2016). Differences in seed mass values represent the competition-colonization (seedling
270 establishment) trade-off (Turnbull *et al.*, 1999) related to the species' dispersal and establishment
271 strategy. Moreover, when analysing multivariate functional differentiation in herbaceous species,
272 these sets of traits were the ones most strongly associated with the two first principal axes
273 (supplementary material Table **S1**), further confirming the importance of these two functional
274 differentiation axes. These findings are broadly consistent with Diaz *et al.* (2016), who found that
275 the main differentiation between species was related to size-related (whole plant and seed) and leaf
276 traits.

277 Ultimately, the individual functional traits related to the populations' temporal patterns are
278 intrinsically linked to how the species adapt to patterns of resource availability and disturbance,

279 both if we analyse the effect of single traits or multi-trait effects (PCoA axes). At the same time, it is
280 interesting to notice that, in our case, combined trait information in the form of plant spectra (i.e.
281 via the PCoA axes) lost some ecological explanatory power compared to specific trait effects. If, on
282 one hand, such multi-trait trade-offs are essential to distinguish the major axis of differentiation
283 among organisms (Diaz et al. 2016), on the other, the independent effect of individual traits might
284 be even more relevant ecologically. This suggests that, for predicting species stability, using specific
285 functional traits could be more effective than using axes of functional variation based on multiple
286 traits. By using axes of functional variation, the traits' individual effects could be blurred or could be
287 missed because both additive and non-additive effects of individual traits (Pistón *et al.*, 2019) are
288 ecologically more relevant than combined multi-trait effects.

289 Leaf traits relate to species adaptations to resource availability. Higher LDMC values, as well
290 as smaller SLA and N content values, correspond to a slow return on investments in nutrients, lower
291 potential relative growth rate, and longer leaf and whole-plant life span (Wright *et al.*, 2004; Garnier
292 *et al.*, 2016). This implies higher potential of buffered population growth. In fact, slow-growing and
293 long-lived species, for example with higher values of LDMC, could have an advantage in
294 unfavourable years due to resources stored from previous, more favourable years, thus maintaining
295 buffered population growth and consequently more stable populations (Májeková *et al.*, 2014;
296 Reich, 2014). Different leaf traits, although broadly linked, capture slightly different aspects of leaf
297 function (Garnier et al., 2016). It follows that they would be differently linked to species growth
298 strategies and their temporal dynamics. Our results show that, although SLA and Leaf N do have an
299 influence, it seems to be secondary (i.e. they have a weaker effect, Table 1, Fig. 1) when compared
300 to LDMC, which is consistently and strongly related to species temporal variability. One explanation
301 is that LDMC is better related to growth rate, compared to the other leaf traits (e.g. Kazakou *et al.*,
302 2006). Another explanation could be that LDMC is probably a trait whose measurement is less likely
303 to be influenced by measurement precision/protocols and therefore it might show less intraspecific
304 variability due to data measurements. At the same time LDMC was also the trait selected, over SLA
305 and Leaf N, in Majekova et al. (2014), where leaf trait measurements from a single location and
306 single working group were more comparable. Possibly LDMC reflects, to a greater extent, a stronger
307 trade-off in growth and defence, and ultimately plant productivity (which is likely linked to the
308 denominator of CV), while SLA and Leaf N are possibly linked to trade-offs more tightly linked to
309 photosynthetic strategies (Smart *et al.*, 2017). Alternatively, LDMC can be also interpreted as a
310 better indicator of response to water stress, which might be an underlying cause of interannual

311 variability (see Majeková *et al.*, 2021). More locally based research is certainly required to define
312 the relative effects of different traits associated to the leaf economic spectrum on population
313 temporal dynamics.

314 Similarly, seed mass consistently appears to have an influence on species temporal variability
315 (Table 1, Fig. 1). This trait relates to the species' adaptations to disturbance patterns and
316 colonization. Larger seed mass means greater resources stored to help the young seedling establish
317 and survive in the face of stress with the cost of short-distance dispersal, while smaller seeds (also
318 in combination with seed shape) are typically related to greater longevity in seed banks and dispersal
319 over longer distances (Thompson *et al.*, 1993; Turnbull *et al.*, 1999; Moles & Westoby, 2006).
320 Therefore, species germinating from seeds with a larger mass are more likely to survive during
321 adverse years and so their populations are more stable in a given site compared to species with
322 smaller seeds, which will tend to maintain their populations through permanence in seed banks,
323 which enables proper germination timing (Venable & Brown, 1988; Metz *et al.*, 2010). In addition,
324 species with greater seed mass might be favoured in communities where gaps are scarce, which are
325 usually dominated by perennial species (with higher LDMC values) and are more stable. Large seeds
326 will tend to remain closer to the mother plant than small seeds, thus increasing the stabilizing effects
327 on populations. Small seeded species still maintain buffered population growth (Pake & Venable,
328 1995), yet their above-ground abundance will be more variable over time, because they usually
329 germinate only in favourable years. This explanation is particularly supported, for example, for
330 short-lived plants (annuals and biennial species together, Table S3), which tend to be less stable
331 over time (Fig. 2b) and are generally associated with the small-seed strategy at a global scale
332 (Westoby, 1998).

333 It is important to consider that the same traits that predicted species variability, using CV,
334 also predicted the components of CV, i.e. species means and standard deviation (SD). Clearly the SD
335 in species fluctuation is inherently increasing with species means, following the so-called Taylor's
336 power law (Lepš, 2004). This leads to the use of CV in the study of stability, as a more "scaled"
337 measure of species variability. At the same time, when the CV is negatively correlated to species
338 mean abundance, as in our case ($r=-0.46$, which corresponds to the case of a slope in the Taylor's
339 power law being lower than 2), it implies that more dominant species tend to fluctuate
340 comparatively less than subordinate species. This is an important observation because this scenario
341 implies that the same type of species that are dominant and likely with greater abundance, e.g. with
342 high LDMC (Smart *et al.*, 2017), are also the more stable ones. Since dominant species were key

343 drivers of the stability of the communities considered in our study (Valencia *et al.*, 2020a) the results
344 of the present study indicate that the same traits that determine species dominance also determine
345 species stability, which is a key message for any attempt to predict both community structure and
346 its potential to buffer environmental fluctuations (de Bello *et al.*, 2021).

347 Despite relatively low R^2 values, our models found consistent evidence of the relationship
348 between continuous traits related to leaf and seed economics and species temporal stability across
349 different biomes (Fig. S4). While we did consider other traits that affected the stability of species,
350 these did not substantially improve the predictive power of models. In particular, adding life span in
351 interaction with the continuous traits analysed in our models did not dramatically improve their
352 performance (see supplementary material Fig. S4). Beyond the obvious effect of life span on species
353 temporal stability, the results in Fig. S4 indicate that although the seed mass effect seems to be
354 obscured or encompassed by the life span trait, our original results linked to traits on the leaf
355 economic spectrum were still relevant for species stability. Further, adding “unmeasured” traits
356 (using phylogeny as a proxy of unmeasured conserved traits, see supplementary material Fig. S5b)
357 did not substantially change the original explained variability. Results showed that some effect from
358 additional traits could be detected, supporting the need for research to identify other important
359 traits that could be related to species stability, for example those linked to vegetative propagation
360 and reproduction, like those specifically related seed dispersal and seed dormancy traits.
361 Importantly, the results where phylogeny was considered were otherwise completely consistent
362 with the original results. This is a first indication that additional (not considered here) quantitative
363 traits might not tremendously increase the explanatory power of the models in a qualitatively
364 important way. As such, further tests using other potentially relevant trait, or traits measured
365 directly in the biomes and locations under study, are surely needed to expand the findings of the
366 present study. Very often traits available in database represent only a small portion of traits actually
367 determining species fitness and the values obtained for those available (generally an average value)
368 might not represent the phenotypic expression in the specific study site under observation. Indeed,
369 one missing factor that could explain the observed variability in species CV could be intraspecific
370 variability in both trait values and species CV, as indicated also by the higher R^2 values when
371 considering the random effects species and dataset. Because of these effects, the present study was
372 not necessarily focussed on maximizing the explained variability but in detecting the most consistent
373 patterns across different biomes, which were detected in the effects of LDMC and seed mass, and

374 opening a new field of research focussed on the search of the best traits, and their combinations, in
375 predicting species stability.

376 An important point to acknowledge is that the compilation of datasets used here is biased
377 towards more temperate biomes, with a predominance of grasslands and open shrublands. This is
378 an artefact of historic sampling bias and dictates available ecological datasets to study interannual
379 ecological stability. Such sampling bias is typically a widespread problem for analyses integrating
380 diverse datasets, where available information can be affected by regional research preferences and
381 funding opportunities for research. These issues are particularly pronounced in long term
382 experiments, where the presence of vegetation with woody species, and particularly tree species,
383 can cause confounding factors in the analyses of temporal dynamics. We dealt with this by using
384 datasets as a random factor and focusing on herbaceous vegetation only, which resulted in patterns
385 apparently consistent across different vegetation types, i.e. also in vegetation with woody species
386 (Fig. S4).

387 Finally, our results show worldwide evidence that species with more conservative leaf
388 economics and greater seed mass are generally more stable, i.e. less variable over time, and
389 therefore confirm theoretical assumptions and are consistent with previous localized empirical
390 evidence on the interdependence between these traits, their relative trade-offs, and population
391 temporal stability (e.g. MacArthur & Wilson, 1967; Májerková *et al.*, 2014). In addition, our results
392 show the global validity of these trade-offs, found across a variety of abiotic and biotic conditions.
393 Overall, our findings contribute to a better understanding of the drivers of plant population
394 temporal stability, which has important implications for the conservation of ecosystem functions
395 over time across the world.

396

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410

411 **Author Contributions**

412 FdB and EV conceived the idea together with LC, EV and TG gathered and collated the data, LC
413 prepared the data, performed the analyses, and wrote the first draft of the manuscript. LG, JL, AE-
414 V, CC, and MM, helped with data preparation and/or statistical analyses. The rest of the authors
415 contributed with data. All the authors actively participated in the writing.

416

417 **Data Availability**

418 The metrics used in the analyses are available at <https://doi.org/10.5281/zenodo.6720583> under
419 CC-BY licence. For access to the LOTVS datasets in full please refer to <https://lotvs.csic.es/>

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560 **Tables and Figures**

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562 **Table 1. Effects of continuous traits on species variability (CV), models comparison.** Model's
 563 summary for both the full model and the reduced model, which test the influence of continuous
 564 traits on the species variability (coefficient of variance in time, CV). The full model contains all the
 565 predictors while the reduced model contains only a subset of the initial predictors. Estimates and
 566 relative standard errors (in brackets) are shown. R² (fixed): variation explained by fixed factors; R²
 567 (total): variation explained by both fixed and random factors. P-values calculated using
 568 Satterthwaite approximation for degrees of freedom. ***p-value<=0.001; **p-value<=0.01; *p-
 569 value<=0.05.

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	Full model	Reduced model
(Intercept)	-0.10 (0.06)	-0.03 (0.04)
Plant height	-0.01 (0.09)	
Leaf N content	0.03 (0.08)	0.06 (0.04)
Leaf P content	0.04 (0.07)	
Seed mass	-0.12 (0.08)	-0.08 * (0.04)
SLA	0.02 (0.09)	0.09 * (0.04)
LDMC	-0.23 ** (0.07)	-0.21 *** (0.04)
SSD	0.06 (0.06)	
N	676	1630
Species	93	395
Datasets	67	77
R ² (fixed)	0.05	0.07
R ² (total)	0.13	0.18

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574 **Table 2. Effects of categorical traits on species variability (CV), models comparison.** Model's
 575 summary for the models testing the influence of categorical traits on the species variability
 576 (coefficient of variance in time, CV). Estimates and relative standard errors (in brackets) are shown.
 577 R^2 (fixed): variation explained by fixed factors; R^2 (total): variation explained by both fixed and
 578 random factors. P-values calculated using Satterthwaite approximation for degrees of freedom.
 579 ***p-value \leq 0.001; **p-value \leq 0.01; *p-value \leq 0.05. Ch: Chamaephyte, Cr: Cryptophyte, H:
 580 Hemicryptophyte, P: Phanerophyte, T: Therophyte
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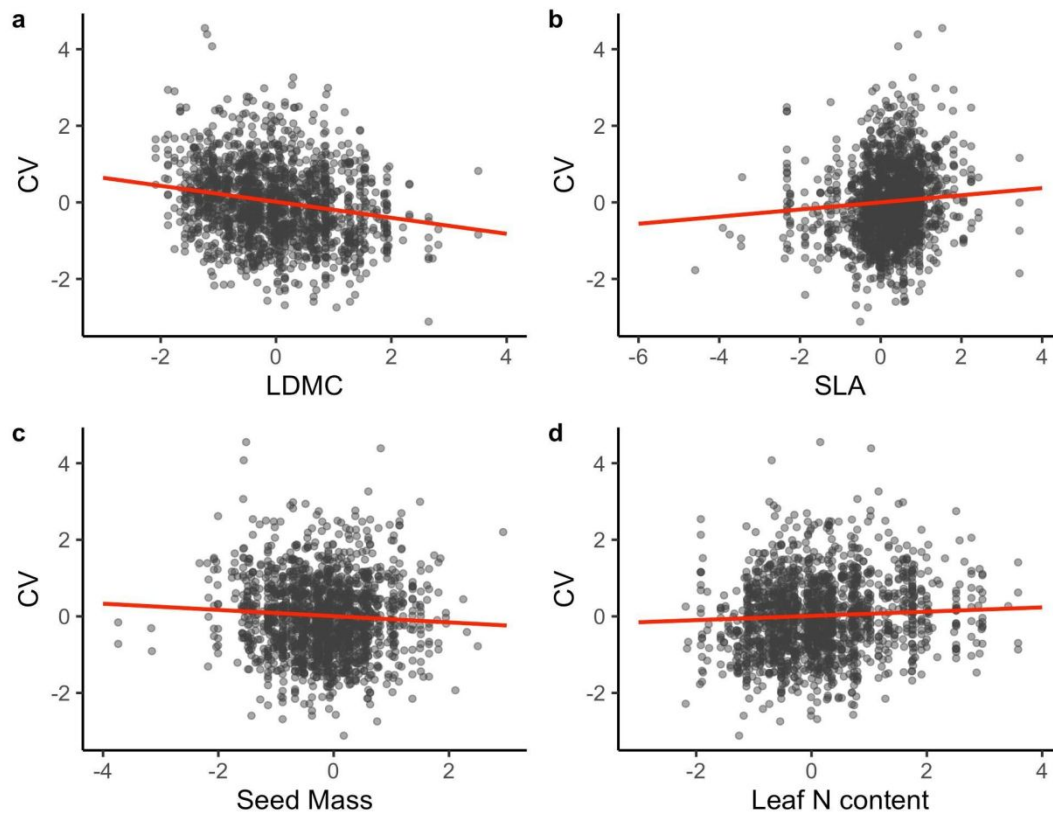
	Woodyness	Life span	Life form	Growth form
non-woody	0.03 (0.02)			
woody	0.03 (0.05)			
annual		0.49 *** (0.05)		
not-annual		-0.06 * (0.02)		
Ch			-0.03 (0.08)	
Cr			-0.09 (0.09)	
H			-0.06 (0.04)	
P			0.18 (0.10)	
T			0.55 *** (0.05)	
fern				-0.27 (0.16)
graminoid				-0.13 *** (0.04)
herb				0.12 *** (0.03)
herb/shrub				-0.21 (0.11)
shrub				-0.01 (0.06)
shrub/tree				-0.03 (0.13)
tree				0.30 * (0.13)
N	3869	3869	2492	3849
Species	1794	1794	990	1779
Datasets	78	78	73	78
R^2 (fixed)	7.04e-07	0.04	0.06	0.02
R^2 (total)	0.23	0.23	0.14	0.22

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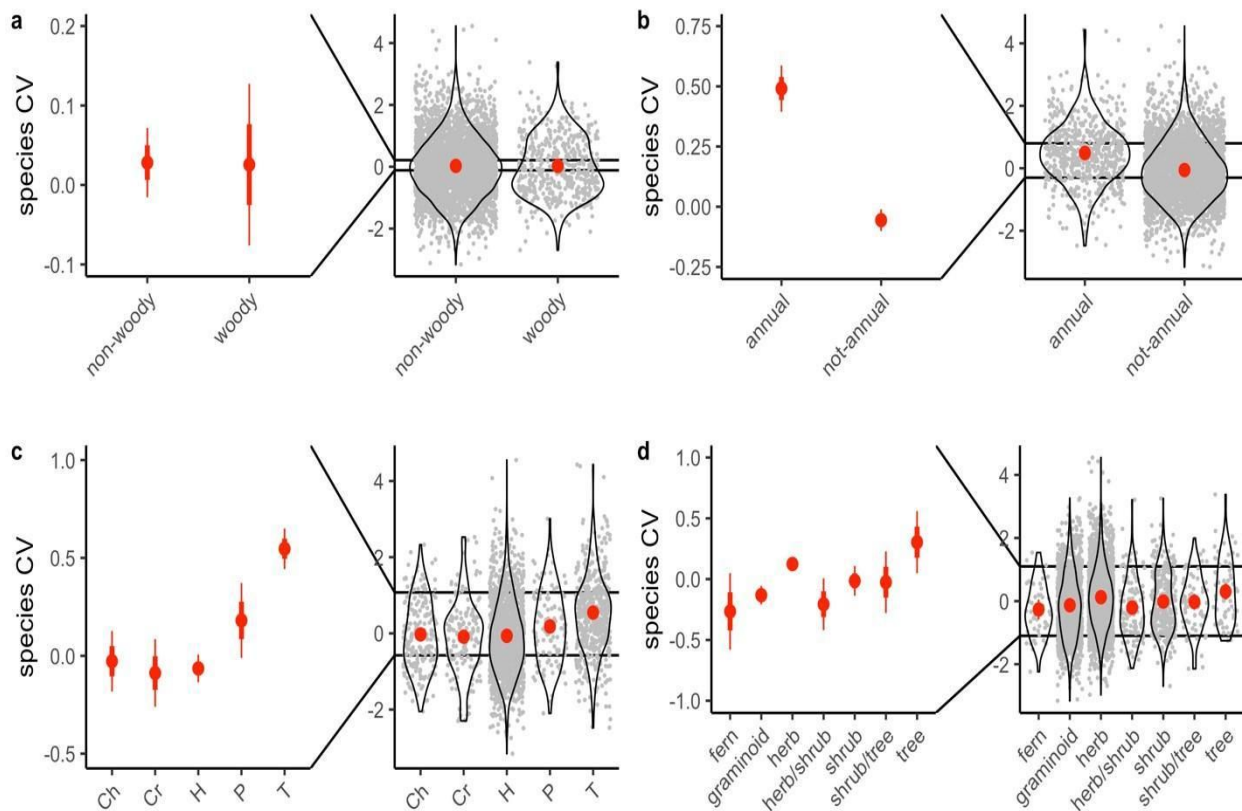
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Figure 1. Effects of continuous traits on species variability (CV). Regression plots of the reduced model showing the effects of leaf dry matter content (LDMC, a), specific leaf area (SLA, b), seed mass (c), and leaf N (d) content on the CV of species.

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Figure 2. Effect of categorical traits on species variability (CV). Here we show results of the models fitted using single categorical traits as predictors for the mean species CV at dataset level (i.e. analogous models as the reduced model in the main text): woodiness (a); life span (b); life form: Ch Chamaephyte, Cr Cryptophyte, H Hemicryptophyte, P Phanerophyte, T Therophyte (c); growth form (d). Estimates and respective confidence intervals (95% by the thin line and 68% by the thick line) are shown in red, which correspond to the summary statistics of each category. Intercept was excluded from the model to better understand the differences across trait categories. The subpanels represent, on the left side, the closeup of the estimates, on the right side, the violin plot for the data used in each model.