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.

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20   **Keywords:** acquisitive; conservative; dispersal; worldwide database; long-term studies; resource

21   use; temporal patterns; variability

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Introduction

Identifying the drivers of temporal stability in plant populations and communities has consequences for maintenance of multiple ecosystem functions over time, including carbon sequestration, fodder resources for livestock, and nutrient cycling (Tilman & Downing, 1994; Hautier *et al.*, 2015; Isbell *et al.*, 2018). One of the main determinants of community stability is the cumulative temporal variability in the abundances of individual species' populations (Thibaut & Connolly, 2013; Hallett e*t al.*, 2014; Májeková *et al.*, 2014). Lower temporal variability in individual population abundances at a given site, and particularly for dominant species, generally increases overall community stability (Lepš *et al.*, 1982, 2018; Pimm, 1984; McCann, 2000). Accordingly, assessing the drivers of temporal variability in populations is necessary to understand and forecast the potential consequences of increasingly common environmental perturbations (Easterling *et al.*, 2000; Lloret *et al.,* 2012).

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

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

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Author Contributions

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

Data Availability

The metrics used in the analyses are available at https://doi.org/10.5281/zenodo.6720583 under 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**

561

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. R^2 (fixed): variation explained by fixed factors; R^2
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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571

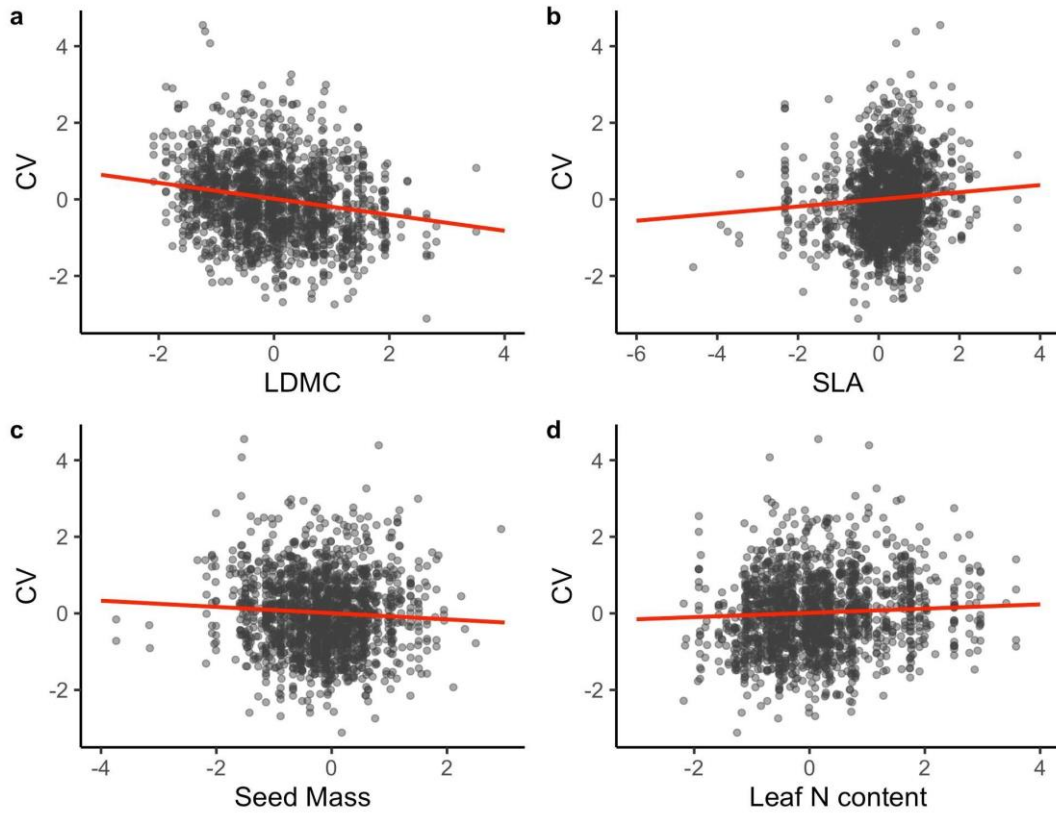|	Full model	Reduced model
(Intercept)	-0.10	-0.03
	(0.06)	(0.04)
Plant height	-0.01	
	(0.09)	
Leaf N content	0.03	0.06
	(0.08)	(0.04)
Leaf P content	0.04	
	(0.07)	
Seed mass	-0.12	-0.08 *
	(0.08)	(0.04)
SLA	0.02	0.09 *
	(0.09)	(0.04)
LDMC	-0.23 **	-0.21 ***
	(0.07)	(0.04)
SSD	0.06	
	(0.06)	
N	676	1630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

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573

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<=0.001; **p-value<=0.01; *p-value<=0.05. Ch: Chamaephyte, Cr: Cryptophyte, H:
580 Hemicryptophyte, P: Phanerophyte, T: Therophyte
581

|	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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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.
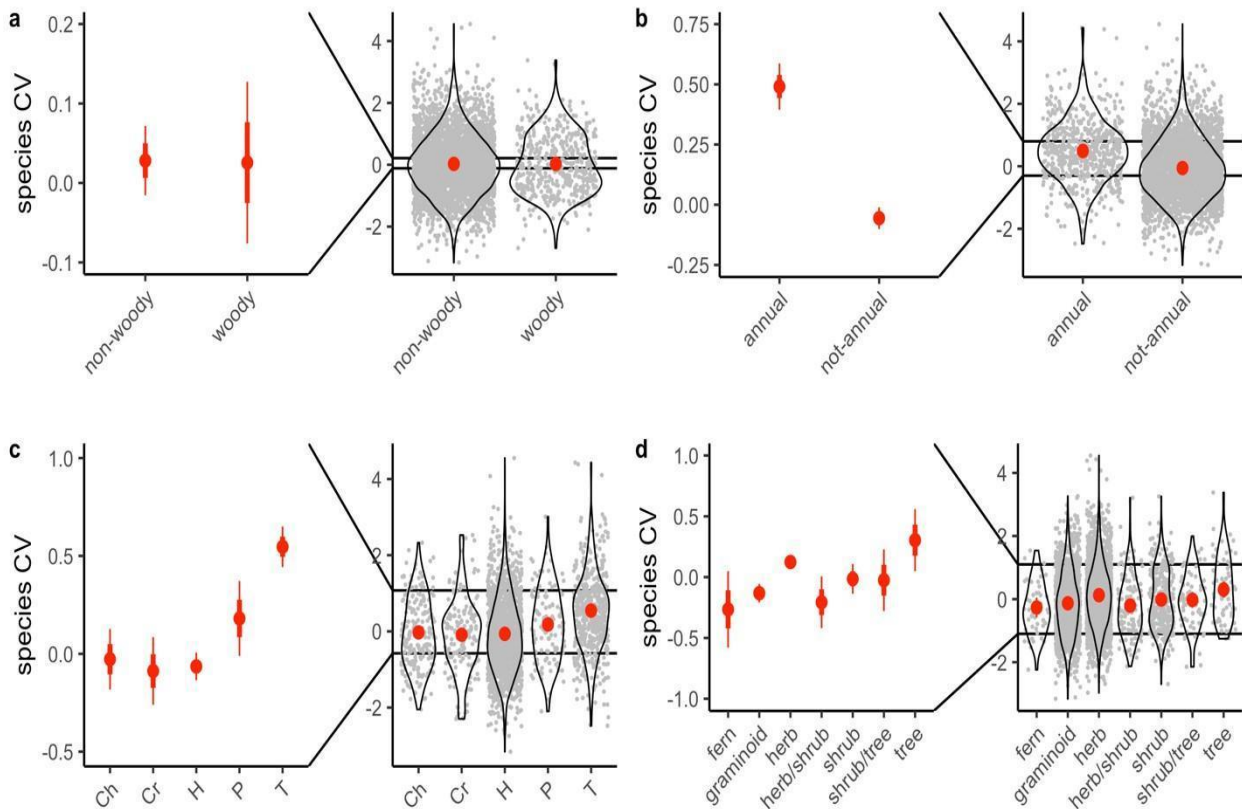
Figure 2. Effect of categorical traits on species variability (CV). Here we show results of the models fitted using single categorical traits as predictors for the mean species CV at dataset level (i.e. analogous models as the reduced model in the main text): woodiness (a); life span (b); life form: 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.