PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Conti L *et al*. 2023 Functional trait trade-offs define plant population stability across different biomes. *Proc. R. Soc. B* **290**: 20230344.
https://doi.org/10.1098/rspb.2023.0344

Received: 25 July 2022
Accepted: 30 May 2023

Subject Category:
Ecology

Subject Areas:
ecology, plant science

Keywords:
acquisitive, conservative, dispersal, long-term studies, temporal patterns, variability

Author for correspondence:
Luisa Conti
e-mail: luisa.conti@gmail.com

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.6688799.

THE ROYAL SOCIETY PUBLISHING

Downloaded from https://royalsocietypublishing.org/ on 27 June 2024

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

Luisa Conti[1,2], Enrique Valencia[3], Thomas Galland[2,4], Lars Götzenberger[2,4], Jan Lepš[4,6], Anna E-Vojtkó[2,4], Carlos P. Carmona[7], Maria Májeková[8], Jiří Danihelka[9,10], Jürgen Dengler[11,12,14], David J. Eldridge[15], Marc Estiarte[16,17], Ricardo García-González[18], Eric Garnier[19], Daniel Gómez[18], Věra Hadincová[10], Susan P. Harrison[20], Tomáš Herben[10,21], Ricardo Ibáñez[22], Anke Jentsch[13], Norbert Juergens[23], Miklós Kertész[24], Katja Klumpp[25], František Krahulec[10], Frédérique Louault[25], Rob H. Marrs[26], Gábor Ónodi[24], Robin J. Pakeman[27], Meelis Pärtel[7], Begoña Peco[28], Josep Peñuelas[16,17], Marta Rueda[29], Wolfgang Schmidt[30], Ute Schmiedel[23], Martin Schuetz[31], Hana Skalova[10], Petr Šmilauer[5], Marie Šmilauerová[4], Christian Smit[32], MingHua Song[33], Martin Stock[34], James Val[15], Vigdis Vandvik[35], David Ward[36], Karsten Wesche[37,38], Susan K. Wiser[39], Ben A. Woodcock[40], Truman P. Young[41,42], Fei-Hai Yu[43], Martin Zobel[7] and Francesco de Bello[44]

[1]Faculty of Environmental Sciences, Czech University of Life Sciences Prague, 16500 Praha–Suchdol, Czech Republic
[2]Institute of Botany of the Czech Academy of Sciences, 37901 Třeboň, Czech Republic
[3]Departament of Biodiversity, Ecology and Evolution, Faculty of Biological Science, Complutense University of Madrid, 28040 Madrid, Spain
[4]Department of Botany, Faculty of Sciences and [5]Department of Ecosystem Biology, Faculty of Science, University of South Bohemia, 37005 České Budějovice, Czech Republic
[6]Institute of Entomology, Czech Academy of Sciences, 37005 Ceske Budejovice, Czech Republic
[7]Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, 50409 Tartu, Estonia
[8]Plant Ecology Group, Institute of Evolution and Ecology, University of Tübingen, 72076 Tübingen, Germany
[9]Department of Botany and Zoology, Masaryk University, 61137 Brno, Czech Republic
[10]Institute of Botany of the Czech Academy of Sciences, 25243 Průhonice, Czech Republic
[11]Vegetation Ecology, Institute of Natural Resource Sciences (IUNR), Zurich University of Applied Sciences (ZHAW), 8820 Wädenswil, Switzerland
[12]Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER) and [13]Disturbance Ecology and Vegetation Dynamics, Bayreuth Center of Ecology and Environmental Research, University of Bayreuth, 95447 Bayreuth, Germany
[14]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103 Leipzig, Germany
[15]Centre for Ecosystem Studies, School of Biological, Earth and Environmental Sciences, University of New South Wales, 2033 Sydney, Australia
[16]CREAF, 08193 Cerdanyola del Vallès, Catalonia, Spain
[17]CSIC, Global Ecology Unit CREAF-CSIC-UAB, 08193 Bellaterra, Catalonia, Spain
[18]Pyrenean Institute of Ecology (IPE-CSIC), 22700 Jaca-Zaragoza, Spain
[19]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[20]Department of Environmental Science and Policy, University of California Davis, CA 95616, USA
[21]Department of Botany, Faculty of Science, Charles University, 12801 Praha, Czech Republic
[22]Department of Environmental Biology, School of Sciences, University of Navarra, 31080 Pamplona, Spain
[23]Research Unit Biodiversity, Evolution and Ecology (BEE) of Plants, Institute of Plant Science and Microbiology, University of Hamburg, 22609 Hamburg, Germany
[24]Institute of Ecology and Botany, Centre for Ecological Research, 2163 Vácrátót, Hungary
[25]Université Clermont Auvergne, INRAE, VetAgro Sup, UMR Ecosystème Prairial, 63000 Clermont Ferrand, France
[26]School of Environmental Sciences, University of Liverpool, Liverpool L69 3GP, UK
[27]The James Hutton Institute, Craigiebuckler, Aberdeen AB15 8QH, UK
[28]Terrestrial Ecology Group (TEG), Department of Ecology, Institute for Biodiversity and Global Change, Autonomous University of Madrid, 28049 Madrid, Spain
[29]Department of Plant Biology and Ecology, University of Seville, 41012 Sevilla, Spain

© 2023 The Author(s) Published by the Royal Society. All rights reserved.

Downloaded from https://royalsocietypublishing.org/ on 27 June 2024

[30]Department of Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, 37077 Germany
[31]Community Ecology, Swiss Federal Institute for Forest, Snow and Landscape Research, 8903 Birmensdorf, Switzerland
[32]Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, 9700 CC Groningen, The Netherlands
[33]Laboratory of Ecosystem Network Observation and Modelling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, 100107 Beijing, People's Republic of China
[34]Wadden Sea National Park of Schleswig-Holstein, 25832 Tönning, Germany
[35]Department of Biological Sciences, University of Bergen, 5006 Bergen, Norway
[36]Department of Biological Sciences, Kent State University, Kent, OH 44243, USA
[37]Botany Department, Senckenberg, Natural History Museum Goerlitz, 02806 Görlitz, Germany
[38]International Institute Zittau, Technische Universität Dresden, Dresden, 03583 Germany
[39]Manaaki Whenua – Landcare Research, Lincoln 7608, New Zealand
[40]UK Centre for Ecology and Hydrology, Crowmarsh Gifford, Wallingford OX10 8BB, UK
[41]Department of Plant Sciences, University of California, Davis, CA 95616, USA
[42]Mpala Research Centre, 100400, Nanyuki, Kenya
[43]Institute of Wetland Ecology and Clone Ecology / Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, 318000 Taizhou, People's Republic of China
[44]CIDE-CSIC, 46113 Valencia, Spain

LC, 0000-0001-8047-1467; EV, 0000-0003-3359-0759; TG, 0000-0003-0883-8871; LG, 0000-0003-3040-2900; JL, 0000-0002-4822-7429; AE-V, 0000-0001-6370-680X; CPC, 0000-0001-6935-4913; MM, 0000-0001-6892-5462; JD, 0000-0002-2640-7867; JD, 0000-0003-3221-660X; DJE, 0000-0002-2191-486X; ME, 0000-0003-1176-8480; RG-G, 0000-0001-5625-8690; EG, 0000-0002-9392-5154; DG, 0000-0002-9738-8720; VH, 0000-0002-3825-1919; SPH, 0000-0001-6278-2181; TH, 0000-0002-6636-0012; RI, 0000-0002-1772-4473; AJ, 0000-0002-2345-8300; NJ, 0000-0003-3211-0549; MK, 0000-0002-3565-4624; KK, 0000-0002-4799-5231; FK, 0000-0001-7706-1723; FL, 0000-0002-9430-4261; RHM, 0000-0002-0664-9420; GÓ, 0000-0003-4308-7997; RJP, 0000-0001-6248-4133; MP, 0000-0002-5874-0138; BP, 0000-0003-2149-1438; JP, 0000-0002-7215-0150; MR, 0000-0002-9754-6258; WS, 0000-0001-5356-4684; US, 0000-0003-4059-6585; HS, 0000-0002-1252-2952; PŠ, 0000-0003-3065-5721; MŠ, 0000-0002-0349-4179; CS, 0000-0002-4044-9473; MHS, 0000-0001-5028-0379; MS, 0000-0002-6649-2912; JV, 0000-0003-4519-4008; VV, 0000-0003-4651-4798; DW, 0000-0002-2705-408X; KW, 0000-0002-0088-6492; SKW, 0000-0002-8938-8181; BAW, 0000-0003-0300-9951; TPY, 0000-0002-7326-3894; F-HY, 0000-0001-5007-1745; MZ, 0000-0001-7957-6704; FdB, 0000-0001-9202-8198

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

1. 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 [1–3]. One of the main determinants of community stability is the cumulative temporal variability in the abundances of individual species' populations [4–6]. Lower temporal variability in individual population abundances at a given site, and particularly for dominant species, generally increases overall community stability [7–10]. Accordingly, assessing the drivers of temporal variability in populations is necessary to understand and forecast the potential consequences of increasingly common environmental perturbations [11,12].

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 [13]). These differences can be described through functional traits that determine how plants respond to environmental factors, affect other trophic levels and influence ecosystem properties [14–16]. 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. [6,17–19]).

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. [20]). 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 [21]). Mostly, such trade-offs have been assessed within the context of community assembly theory and eco-evolutionary models for niche differentiation (e.g. [22–24]). 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 [25].

At the same time, different specific trade-offs can also underlie differences in temporal variations in species' abundances, both within and between community types. For example, species that are able to respond quickly to environmental variability, i.e. acquisitive resource-use strategy, fast-growing species that invest in organs for rapid resource acquisition and/or high dispersal ability, should sustain higher temporal variation in population size, and will be favoured in sites where disturbance and/or environmental instability determine a fluctuation in resources [13,26,27]. By contrast, species adapted to endure environmental variability

Downloaded from https://royalsocietypublishing.org/ on 27 June 2024

(i.e. conservative resource-use strategy, slow-growing and long-lived species that invest in structural tissues and permanence) are thought to persist during unfavourable periods due to resources stored from previous, more favourable years [28], and will exhibit less temporal variability [13,29]. These species are expected to be favoured in more stable and predictable environments [30].

It remains unclear though whether the potential relationship between species' traits and species' stability would be detected across different biomes and through differences in single traits or combined axes of differentiation that incorporate multiple traits [20,26,31]. Several ecological strategy schemes, such as the classic r/K selection [13] and C-S-R [21] theories, as well as the leaf-height-seed (LHS) scheme [26], can theoretically help predict how functional trade-offs determine species' temporal strategies and their fitness across different types of environments. The LHS scheme for instance is based on three independent plant traits which should provide key proxies for independent trade-offs in plants (stress adaptation, competition and response to disturbance respectively; [26]). Interestingly, only a few empirical studies have linked differences in temporal strategies to functional traits within plant communities [6,17,18,32,33]. For example, Májeková *et al*. [6] empirically confirmed that herbaceous species with a more conservative resource-use strategy (i.e. those with higher leaf dry matter content—LDMC) have more stable populations over time. A similar relationship was found at the community level, where communities including a greater abundance of species with high LDMC were more stable [34,35]. A recent global meta-analysis of sown grasslands, although based on short-term experiments, suggested that an increase in the abundance of rapidly growing species can destabilize community biomass over time [33]. This is supported by empirical demonstrations that, in natural vegetation, community stability is predicted by the functional traits of the dominant species rather than by species diversity *per se* [7]. Further, only Májeková *et al*. [6] tested whether trait-based predictions of population temporal variability were consistent across different management regimes, i.e. fertilization and competitor-removal treatments, generally finding minor differences and consistent predictions for LDMC. Ultimately, global empirical evidence of a general link between quantitative functional traits and the temporal variability of populations, and whether this link is maintained despite differences in community types and environmental conditions, is still missing [27].

Here, using an extended compilation of long-term, recurrently monitored vegetation plots, encompassing different habitat types around the world (https://lotvs.csic.es) [36], we determine which plant traits better predict the temporal stability of plant populations. We expect that populations of species with more acquisitive and higher dispersal-ability traits will tend to be more variable over time, while those of species with more conservative trait values and lower dispersal ability will tend to be more stable over time. We also expect to find empirical evidence of the generality of these relationships.

2. Materials and methods

(a) Plots and population stability

We used 78 datasets contained in the LOTVS collection of temporal vegetation data. These consist of a total of 7396 permanent plots of natural and semi-natural vegetation that have been consistently sampled for periods of between six and 99 years, depending on the dataset (electronic supplementary material, table S2) [36,37]. These datasets were collected from study sites in different biomes that span the globe, in 18 different countries: Australia, China, Czech Republic, Estonia, France, Germany, Hungary, Kenya, Mongolia, Netherlands, New Zealand, Norway, Russia, South Africa, Spain, Switzerland, United Kingdom and USA. They differ in sampling method (e.g. abundance measured as above-ground biomass, visual species cover estimates and species individual frequencies), plot size and study duration. The studies that generated the datasets sampled different types of vegetation (predominantly grasslands but also shrublands and forests) and covered a wide array of biomes, with mean annual precipitation spanning from 140 mm to 2211 mm, highest temperature of the warmest month spanning from 11.3°C to 35.7°C and lowest temperature of the coldest month spanning from −35.3°C to 7.7°C (electronic supplementary material, table S2).

First, for each plot, we quantified the inter-annual variability in the size of each species's population using the coefficient of variation (CV) of abundance over time, i.e. the standard deviation (s.d.) of species abundance over mean species abundance [6,27]. Since a fundamental differentiation between growing strategies corresponds to whether a species is woody or non-woody [20,28], we focused the main analyses on non-woody species only. This meant we excluded any species belonging to forest overstoreys (i.e. trees and shrubs), woody species' seedlings and any other species defined as woody when present in the plots. Moreover, based on the collected data available, in many plots, we could not distinguish adult woody individuals from seedlings, with seedlings being the most likely cause of high variability in woody species' CV values (figure 2*a*). Nevertheless, we tested differences in CV values between woody and non-woody species in our data, and we considered a possible influence of the presence of woody overstorey on the CV values (see data analysis).

To avoid using biased CV values for very sporadic species (increased CV), we also excluded those species that occurred in fewer than 30% of the sampling events across the time series for a given plot [6]. Further, to account for variability in CV values between and within the datasets, mostly due to differences in abiotic, biotic and management conditions, we calculated the average CV value for each species in each dataset, standardizing and scaling these averages within each dataset (*z*-scores). This resulted in a total of 3397 species per dataset CV values. To account for potential effects of temporal directional trends in vegetation affecting CV [38], we also computed a detrended version of CV (CVt3) which gave very similar results to the basic CV calculations (see electronic supplementary material, figure S1).

(b) Functional traits

For all the species in our dataset, we collected trait information from the TRY global database [39]. We considered different functional traits representing different components of major plants' growing strategies [26]. Regarding categorical traits, we considered lifespan (annual and non-annual), life form, woodiness (woody and non-woody) and growth form. For continuous traits, we analysed plant height, seed mass, specific stem density, LDMC, specific leaf area (SLA), leaf nitrogen content per unit mass and leaf phosphorus content per unit mass (see [40] for trait name nomenclature and definitions). Besides considering the effects of these traits separately, we also evaluated the effect of both categorical traits and quantitative traits together (see electronic supplementary material, figure S4) and the effect of quantitative traits beyond categorical traits. Furthermore, considering phylogeny as a proxy of conserved functional traits, we considered the effect of potentially unmeasured traits (see electronic supplementary material, figure S5b).

Downloaded from https://royalsocietypublishing.org/ on 27 June 2024

For each species, we averaged trait values across all standard measurements obtained from TRY, excluding those performed under explicit treatments or on juveniles, and outliers. The traits that were log-transformed (using natural logarithm) to achieve a normal distribution. For details on the traits used, their summary statistics, their correlations and their coverage in each dataset, see electronic supplementary material, table S3. To take into account multi-variate trade-offs between species, we also considered axes of functional variation derived from multi-variate analyses (principal coordinates analysis, PCoA). The traits considered were weakly inter-correlated, with the two major axes of trait differentiation from PCoA, linked mainly to LDMC and seed mass (see electronic supplementary material, table S1 for details). The taxonomic names follow the nomenclature of 'The Plant List' (www.theplantlist.org). Nomenclature was standardized using the R package 'Taxonstand' [41].

(c) Data analyses

To quantify how the considered traits were linked to species CV, we used linear mixed effect models ('lmer' function in R package 'lme4', [42]). As a response variable, we used the mean CV for each species in each dataset, standardized as mentioned above. To analyse the effect of the continuous traits, we fitted a single model. As predictors, we included all the continuous traits listed above, scaled and centred. To account for the taxonomic and spatial structure of the data, we included both species identity and dataset identifier as random intercept factors in all of the models. We visually checked the compliance of all of the models residuals with normality and homoscedasticity. To assess the goodness-of-fit of the full model, fixed (i.e. marginal) and total (i.e. conditional) R^2 were calculated [43,44]. To define which among the continuous traits were more relevant for species stability, we compared the fixed R^2 of different models, each differing in the subset of predictors that were included. These different models were fitted to different datasets because of the presence of missing values in the trait data. We used R^2 as a unifying measure of goodness of fit (i.e. as a measure of how well the different models explain the variability in the different datasets). Using this approach, we selected the model that had the highest fixed R^2. In the present work, we focused on significant terms in the reduced model. For completeness, we also compared AIC of full and reduced models by fitting them to the same subset of the data (i.e. we fitted the reduced model to the dataset of the full model). We found that the AIC was indeed lower when using a subset of the trait variables (AIC of the full model was 1939.2, AIC of the reduced model using the same data frame was 1934.6). Separate models were fitted to clarify the influence of categorical traits on the stability of species, each using either woodiness, lifespan, life form or growth form as predictors. In these models, we excluded the intercept, to better see the differences between the trait categories. In addition, analogous models were run also on the two components determining species' CV separately, i.e. mean abundance and s.d. of abundance in time, also standardizing these variables within each dataset (electronic supplementary material, figure S1).

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

Table 1. Effects of continuous traits on species variability (CV), models comparison. Model's summary for both the full model and the reduced model, which test the influence of continuous traits on the species variability (coefficient of variance in time, CV). The full model contains all the predictors while the reduced model contains only a subset of the initial predictors. Estimates and relative s.e. (in brackets) are shown. R^2 (fixed): variation explained by fixed factors; R^2 (total): variation explained by both fixed and random factors. *p*-values calculated using Satterthwaite approximation for degrees of freedom. ***$p \leq 0.001$; **$p \leq 0.01$; *$p \leq 0.05$.

	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

3. Results

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

We found significant negative coefficients with species CV for LDMC and for seed mass (table 1; figure 1). These coefficients indicate that species with greater LDMC and greater seed mass were more stable (i.e. lower CV values; figure 1*a*). By contrast, we found positive coefficients for SLA and Leaf N content, although the effect was statistically significant only for SLA. For these traits, the larger the trait value, the higher the species CV and therefore the less stable the species populations (figure 1*b*,*d*). The effect of these traits was consistent across datasets (low deviation of

Downloaded from https://royalsocietypublishing.org/ on 27 June 2024

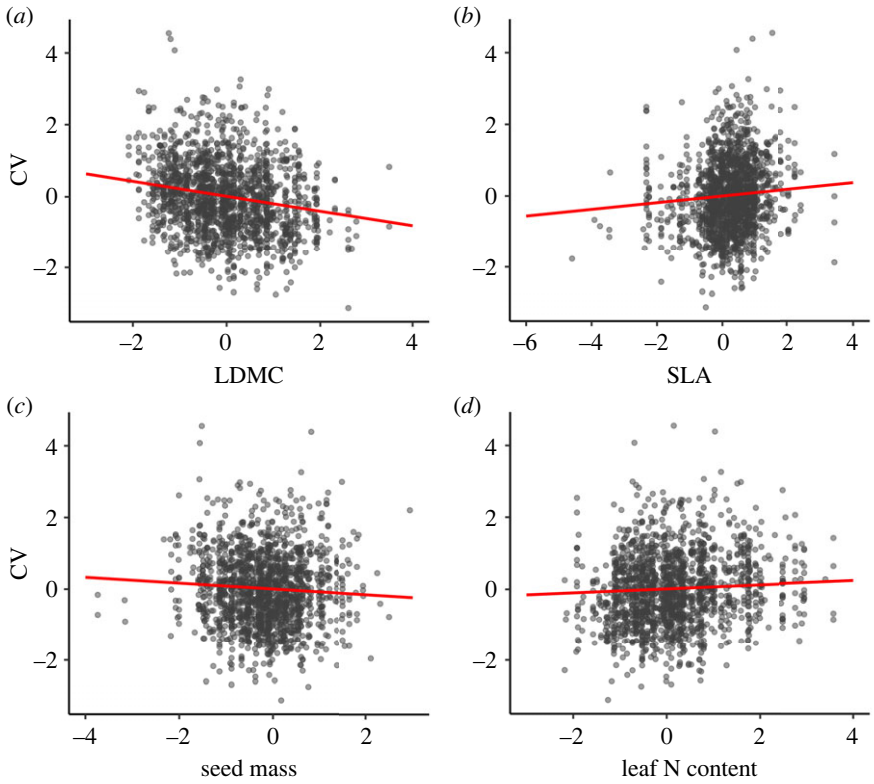

Figure 1. Effects of continuous traits on species variability (CV). Regression plots of the reduced model showing the effects of LDMC (*a*), SLA (*b*), seed mass (*c*) and leaf N (*d*) content on the CV of species.

the datasets' random slope effect compared to the main effect slope for both the models using LDMC and seed mass; electronic supplementary material, figure S3). Since the variability explained by individual traits was low (R^2 = 0.07 for fixed effects in the reduced model using the quantitative traits, table 1), we assessed the role of combining quantitative traits into multi-variate axes, categorical traits, or by considering phylogeny.

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

Categorical traits provided some improved predictions compared of using continuous traits, both influencing CV alone (table 2) and in combination with quantitative traits (electronic supplementary material, figure S4). Herbaceous species with longer lifespan (i.e. perennial and biennial) tended to have a lower CV (fixed $R^2 = 0.04$; table 2). Adding lifespan to the models with quantitative traits, however, did improve predictions only to 0.10 (fixed R^2). Most importantly, the interaction between lifespan and the quantitative traits considered was not significant, indicating that, for example, LDMC was a good predictor of stability for both non-annual and annual species. Woody species, trees and shrubs also had low CV scores (although with very low fixed $R^2 = 7.04 \times 10^{-07}$). Finally, after accounting for phylogeny (i.e. adding phylogenetic eigenvectors to 'correct' CV values), there was no evidence for an overall improvement in model explanatory power (fixed R^2 was 0.01) nor did this substantially modify the results (see electronic supplementary material, figure S5). At the same time, the phylogenetic signal not accounted for by the considered traits (decoupled phylogenetic information; [45]; electronic supplementary material, figure S5), used here as a proxy of unmeasured traits, did not change the original explained variability (fixed R^2 stayed at 0.07).

4. Discussion

By analysing a large worldwide compilation of permanent vegetation plot records, we confirmed the generality and consistency of theoretical predictions relating key functional traits to plant population stability over time. We specifically found that the species with greater LDMC and a larger seed mass were the most stable over time. Ultimately, these

Downloaded from https://royalsocietypublishing.org/ on 27 June 2024

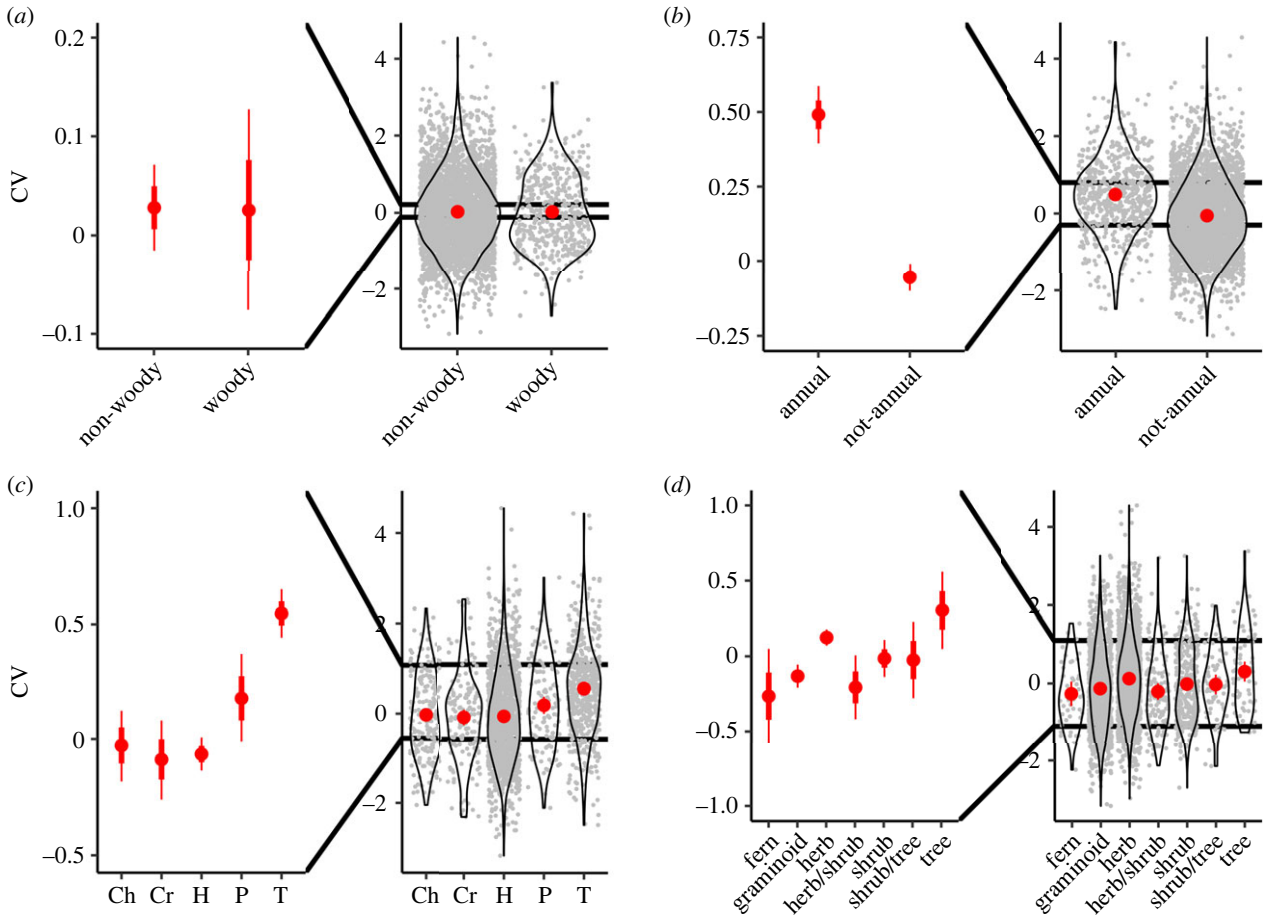

Figure 2. Effect of categorical traits on species variability (CV). Here we show results of the models fitted using single-categorical traits as predictors for the mean species CV at dataset level (i.e. analogous models as the reduced model in the main text): (*a*) woodiness; (*b*) lifespan; (*c*) life form (Ch: chamaephyte, Cr: cryptophyte, H: hemicryptophyte, P: phanerophyte, T: therophyte); (*d*) growth form. 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.

results suggest that common functional trade-offs related to resource use and dispersal consistently influence herbaceous plant population stability across different biomes worldwide. While the results demonstrate that simple plant traits can help, consistently, in predicting the stability of individual species, and ultimately of plant communities, the variability explained by these traits was low, despite accounting for other key traits like lifespan or using phylogeny as a proxy of unmeasured traits. Further research is therefore necessary to integrate and evaluate the role of intraspecific trait variability and other potentially relevant traits, generally not available in trait databases, in modulating species stability.

We identified two functional trade-offs that influence species stability. Specifically, differences associated with the leaf economic spectrum (in our case linked to LDMC, SLA and N content values) define trade-offs in terms of slow-fast resource acquisition [20,25]. Differences in seed mass values represent the competition-colonization (seedling establishment) trade-off [46] related to the species' dispersal and establishment strategy. Moreover, when analysing multi-variate functional differentiation in herbaceous species, these sets of traits were the ones most strongly associated with the two first principal axes (electronic supplementary material, table S1), further confirming the importance of these two functional differentiation axes. These findings are broadly consistent with Díaz *et al.* [20], who found that the main differentiation between species was related to size-related (whole plant and seed) and leaf traits.

Ultimately, the individual functional traits related to the populations' temporal patterns are intrinsically linked to how the species adapt to patterns of resource availability and disturbance, both if we analyse the effect of single traits or multi-trait effects (PCoA axes). At the same time, it is interesting to notice that, in our case, combined trait information in the form of plant spectra (i.e. via the PCoA axes) lost some ecological explanatory power compared to specific trait effects. If, on one hand, such multi-trait trade-offs are essential to distinguish the major axis of differentiation among organisms [20], on the other, the independent effect of individual traits might be even more relevant ecologically. This suggests that, for predicting species stability, using single functional traits could be more effective than using axes of functional variation based on multiple traits. By using axes of functional variation, the traits' individual effects could be blurred or could be missed because both additive and non-additive effects of single traits [47] are ecologically more relevant than combined multi-trait effects.

Leaf traits relate to species adaptations to resource availability. Higher LDMC values, as well as smaller SLA and N content values, correspond to a slow return on investments in nutrients, lower potential relative growth rate and longer leaf and whole-plant lifespan [16,25]. This implies higher potential of buffered population growth. In fact, slow-growing and long-lived species, for example with higher values of LDMC, could have an advantage in unfavourable years due to resources stored from previous, more favourable years,

Downloaded from https://royalsocietypublishing.org/ on 27 June 2024

Table 2. Effects of categorical traits on species variability (CV): comparison of the models testing the influence of categorical traits on the species variability (coefficient of variance in time, CV). Estimates and relative s.e. (in brackets) are shown. R^2 (fixed): variation explained by fixed factors; R^2 (total): variation explained by both fixed and random factors. *p*-values calculated using Satterthwaite approximation for degrees of freedom. ***$p \leq 0.001$; **$p \leq 0.01$; *$p \leq 0.05$. Ch: chamaephyte, Cr: cryptophyte, H: hemicryptophyte, P: phanerophyte, T: therophyte.

	woodyness	lifespan	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)	7.04×10^{-07}	0.04	0.06	0.02
R^2 (total)	0.23	0.23	0.14	0.22

thus maintaining buffered population growth and consequently more stable populations [6,28]. Different leaf traits, although broadly linked, capture different aspects of leaf function [16]. It follows that they would be differently linked to species growth strategies and their temporal dynamics. Our results show that, although SLA and Leaf N do have an influence, it seems to be secondary (i.e. they have a weaker effect; table 1; figure 1) when compared to LDMC, which is consistently and strongly related to species temporal variability. One explanation is that LDMC is better related to growth rate, compared to the other leaf traits (e.g. [48]). Another explanation could be that LDMC is probably a trait whose measurement is less likely to be influenced by measurement precision/protocols and therefore it might show less

Downloaded from https://royalsocietypublishing.org/ on 27 June 2024

intraspecific variability due to data measurements. At the same time, LDMC was also the trait selected, over SLA and Leaf N, in Májeková *et al*. [6], where leaf trait measurements from a single location and single working group were more comparable. Possibly LDMC reflects, to a greater extent, a stronger trade-off in growth and defence, and ultimately plant productivity (which is likely linked to the denominator of CV), while SLA and Leaf N are possibly linked to trade-offs more tightly linked to photosynthetic strategies [49]. Alternatively, LDMC can be also interpreted as a better indicator of response to water stress, which might be an underlying cause of inter-annual variability (see [6]). More locally based research is certainly required to define the relative effects of different traits associated with the leaf economic spectrum on population temporal dynamics.

Similarly, seed mass consistently appears to have an influence on species temporal variability (table 1; figure 1). This trait relates to the species' adaptations to disturbance patterns and colonization. Larger seed mass means greater resources stored to help the young seedling establish and survive in the face of stress with the cost of short-distance dispersal, while smaller seeds (also in combination with seed shape) are typically related to greater longevity in seed banks and dispersal over longer distances [46,50,51]. Therefore, species germinating from seeds with a larger mass are more likely to survive during adverse years and so their populations are more stable in a given site compared to species with smaller seeds, which will tend to maintain their populations through permanence in seed banks, which enables proper germination timing [18,52]. In addition, species with greater seed mass might be favoured in communities where gaps are scarce, which are usually dominated by perennial species (with higher LDMC values) and are more stable. Large seeds will tend to remain closer to the mother plant than small seeds, thus increasing the stabilizing effects on populations. Small-seeded species still maintain buffered population growth [53], yet their above-ground abundance will be more variable over time, because they usually germinate only in favourable years. This explanation is particularly supported, for example, for short-lived plants (annuals and biennial species together, electronic supplementary material, table S3), which tend to be less stable over time (figure 2*b*) and are generally associated with the small-seed strategy at a global scale [26].

It is important to consider that the same traits that predicted species variability, using CV, also predicted the components of CV, i.e. species means and s.d. Clearly the s.d. in species fluctuation is inherently increasing with species means, following the so-called Taylor's power law [54]. This leads to the use of CV in the study of stability, as a more 'scaled' measure of species variability. At the same time, when the CV is negatively correlated to species mean abundance, as in our case ($r = -0.46$, which corresponds to the case of a slope in the Taylor's power law being lower than 2), it implies that more dominant species tend to fluctuate comparatively less than subordinate species. This is an important observation because this scenario implies that the same type of species that are dominant and likely with greater abundance, e.g. with high LDMC [49], is also the more stable ones. Since dominant species were key drivers of the stability of the communities considered in our study [37], the results of the present study indicate that the same traits that determine species dominance also determine species stability, which is a key message for any attempt to predict both community structure and its potential to buffer environmental fluctuations [27].

Despite low R^2 values, our models found consistent evidence of the relationship between continuous traits related to leaf and seed economics and species temporal stability across different biomes (electronic supplementary material, figure S4). While we did consider other traits that affected the stability of species, these did not substantially improve the predictive power of models. In particular, adding lifespan in interaction with the continuous traits analysed in our models improves their performance only to a small extent (see electronic supplementary material, figure S4). Beyond the obvious effect of lifespan on species temporal stability, the results in electronic supplementary material, figure S4 indicate that although the seed mass effect seems to be obscured or encompassed by the lifespan trait, our original results linked to traits on the leaf economic spectrum were still relevant for species stability. Further, adding 'unmeasured' traits (using phylogeny as a proxy of unmeasured conserved traits, see electronic supplementary material, figure S5b) did not substantially change the original explained variability. Results showed that some effect from additional traits could be detected, supporting the need for research to identify other important traits that could be related to species stability, for example, those linked to vegetative propagation and reproduction, like those specifically related seed dispersal and seed dormancy traits. Importantly, the results where phylogeny was considered were otherwise completely consistent with the original results. This is a first indication that additional (not considered here) quantitative traits might not increase the explanatory power of the models in a qualitatively important way. As such, further tests using other potentially relevant trait, or traits measured directly in the biomes and locations under study, are surely needed to expand the findings of the present study. Very often traits available in database represent only a small portion of traits actually determining species fitness and the values obtained for those available (generally an average value) might not represent the phenotypic expression in the specific study site under observation. Indeed, one missing factor that could explain the observed variability in species CV could be intraspecific variability in both trait values and species CV, as indicated also by the higher R^2 values when considering the random effects species and dataset. Because of these effects, the present study was not necessarily focused on maximizing the explained variability but in detecting the most consistent patterns across different biomes, which were detected in the effects of LDMC and seed mass, and opening a new field of research focused on the search of the best traits, and their combinations, in predicting species stability.

An important point to acknowledge is that the compilation of datasets used here is biased towards more temperate biomes, with a predominance of grasslands and open shrublands. This is an artefact of historic sampling bias and dictates available ecological datasets to study inter-annual ecological stability. Such sampling bias is typically a widespread problem for analyses integrating diverse datasets, where available information can be affected by regional research preferences and funding opportunities for research. These issues are particularly pronounced in long-term experiments, where the presence of vegetation with woody species, and particularly tree species, can cause confounding factors in the analyses of temporal dynamics. We dealt with this by using datasets as a random factor and focusing on herbaceous

Downloaded from https://royalsocietypublishing.org/ on 27 June 2024

vegetation only, which resulted in patterns apparently consistent across different vegetation types, i.e. also in vegetation with woody species (electronic supplementary material, figure S4).

Finally, our results show worldwide evidence that species with more conservative leaf economics and greater seed mass are generally more stable, i.e. less variable over time, and therefore confirm theoretical assumptions and are consistent with previous localized empirical evidence on the interdependence between these traits, their relative trade-offs and population temporal stability (e.g. [6,13]). In addition, our results show the global validity of these trade-offs, found across a variety of abiotic and biotic conditions. Overall, our findings contribute to a better understanding of the drivers of plant population temporal stability, which has important implications for the conservation of ecosystem functions over time across the world.

Data accessibility. The metrics used in the analyses are available at https://doi.org/10.5281/zenodo.7978254 [55] under CCBY licence. For access to the LOTVS datasets in full please refer to https://lotvs.csic.es/

The data are provided in the electronic supplementary material [56].

Authors' contributions. L.C.: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft and writing—review and editing; E.V.: conceptualization, data curation, methodology and writing—review and editing; T.G.: conceptualization, data curation, methodology and writing—review and editing; L.G.: conceptualization, data curation, formal analysis, funding acquisition, methodology and writing—review and editing; J.L.: conceptualization, funding acquisition, methodology and writing—review and editing; A.E.: data curation, methodology and writing—review and editing; C.P.C.: data curation, methodology and writing—review and editing; M.M.: methodology and writing—review and editing; J.Da.: data curation and writing—review and editing; J.De.: data curation and writing—review and editing; D.J.E.: data curation and writing—review and editing; M.E.: data curation and writing—review and editing; R.G.-G.: data curation and writing—review and editing; E.G.: data curation and writing—review and editing; D.G.: data curation and writing—review and editing; V.H.: data curation and writing—review and editing; S.P.H.: data curation and writing—review and editing; T.H.: data curation and writing—review and editing; R.I.: data curation and writing—review and editing; A.J.: data curation and writing—review and editing; N.J.: data curation and writing—review and editing; M.K.: data curation and writing—review and editing; K.K.: data curation and writing—review and editing; F.K.: data curation and writing—review and editing; F.L.: data curation and writing—review and editing; R.H.M.: data curation and writing—review and editing; G.Ó.: data curation and writing—review and editing; R.J.P.: data curation and writing—review and editing; M.P.: data curation and writing—review and editing; B.P.: data curation and writing—review and editing; J.P.: data curation and writing—review and editing; M.R.: data curation and writing—review and editing; W.S.: data curation and writing—review and editing; U.S.: data curation and writing—review and editing; M.Sc.: data curation and writing—review and editing; H.S.: data curation and writing—review and editing; P.Š.: data curation and writing—review and editing; M.Š.: data curation and writing—review and editing; C.S.: data curation and writing—review and editing; M.So.: data curation and writing—review and editing; M.St.: data curation and writing—review and editing; J.V.: data curation and writing—review and editing; V.V.: data curation and writing—review and editing; D.W.: data curation and writing—review and editing; K.W.: data curation and writing—review and editing; S.K.W.: data curation and writing—review and editing; B.A.W.: data curation and writing—review and editing; T.P.Y.: data curation and writing—review and editing; F.-H.Y.: data curation and writing—review and editing; M.Z.: data curation and writing—original draft; F.d.B.: conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, resources, supervision, writing—original draft and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This research was funded by Czech Science Foundation Grant GACR16-15012S and Czech Academy of Sciences Grant RVO 67985939 and by the Spanish Plan Nacional de I + D + i (project PGC2018-099027-B-I00). R.J.P. was supported by the Scottish Government's Rural and Environmental Sciences and Analytical Services division. M.P. and C.P.C. were supported by the Estonian Research Council grant (grant nos. PRG609 and PSG293). M.P. and M.Z. were supported by the European Regional Development Fund (Centre of Excellence EcolChange). S.K.W. was supported by the Strategic Science Investment Fund of the New Zealand Ministry of Business, Innovation and Employment. E.V. was funded by the 2017 program for attracting and retaining talent of Comunidad de Madrid (grant no. 2017-T2/AMB-5406). B.A.W. is funded by NERC under AgZero + NE/W005050/1 and RestREco NE/V006444/1. R.M. was supported by Defra and the Leverhulme Trust. T.P.Y. was supported by the U.S. National Science Foundation (19-31224). J.P. was supported by the Fundación Ramón Areces grant CIVP20A6621.

Acknowledgements. We thank the editor and the anonymous referees for their contributions and inputs which helped improving this work.

References

1. Tilman D, Downing JA. 1994 Biodiversity and stability in grasslands. *Nature* **367**, 363–365. (doi:10.1038/367363a0)
2. Hautier Y, Tilman D, Isbell F, Seabloom EW, Borer ET, Reich PB. 2015 Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science* **348**, 336–340. (doi:10.1126/science.aaa1788)
3. Isbell F, Cowles J, Dee LE, Loreau M, Reich PB, Gonzalez A, Hector A, Schmid B. 2018 Quantifying effects of biodiversity on ecosystem functioning across times and places. *Ecol. Lett.* **21**, 763–778. (doi:10.1111/ele.12928)
4. Thibaut LM, Connolly SR. 2013 Understanding diversity-stability relationships: towards a unified model of portfolio effects. *Ecol. Lett.* **16**, 140–150. (doi:10.1111/ele.12019)
5. Hallett LM *et al.* 2014 Biotic mechanisms of community stability shift along a precipitation gradient. *Ecology* **95**, 1693–1700. (doi:10.1890/13-0895.1)
6. Májeková M, de Bello F, Doležal J, Lepš J. 2014 Plant functional traits as determinants of population stability. *Ecology* **95**, 2369–2374. (doi:10.1890/13-1880.1)
7. Lepš J, Osbornová-Kosinová J, Rejmánek M. 1982 Community stability, complexity and species life history strategies. *Vegetatio* **50**, 53–63. (doi:10.1007/BF00120678)
8. Lepš J, Májeková M, Vítová A, Doležal J, de Bello F. 2018 Stabilizing effects in temporal fluctuations: management, traits, and species richness in high-diversity communities. *Ecology* **99**, 360–371. (doi:10.1002/ecy.2065)
9. Pimm S. 1984 The complexity and stability of ecosystems. *Nature* **307**, 321–326. (doi:10.1038/307321a0)
10. McCann KS. 2000 The diversity–stability debate. *Nature* **405**, 228–233. (doi:10.1038/35012234)
11. Easterling DR, Evans JL, Groisman PY, Karl TR, Kunkel KE, Ambenje P. 2000 Observed variability and trends in extreme climate events: a brief review. *Bull. Am. Meteorol. Soc.* **81**, 417–425. (doi:10.1175/1520-0477(2000)081<0417:OVATIE>2.3.CO;2)
12. Lloret F, Escudero A, Iriondo JM, Martínez-Vilalta J, Valladares F. 2012 Extreme climatic events and vegetation: the role of stabilizing processes. *Glob. Change Biol.* **18**, 797–805. (doi:10.1111/j.1365-2486.2011.02624.x)

Downloaded from https://royalsocietypublishing.org/ on 27 June 2024

13. MacArthur RH, Wilson EO. 1967 *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
14. Lavorel S, Garnier E. 2002 Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* **16**, 545–556. (doi:10.1046/j.1365-2435.2002.00664.x)
15. Kattge J *et al.* 2011 TRY - a global database of plant traits. *Glob. Change Biol.* **17**, 2905–2935. (doi:10.1111/j.1365-2486.2011.02451.x)
16. Garnier E, Navas M, Grigulis K. 2016 *Plant functional diversity: organism traits, community structure, and ecosystem properties*. Oxford, UK: Oxford University Press.
17. Angert AL, Huxman TE, Chesson P, Venable DL. 2009 Functional tradeoffs determine species coexistence via the storage effect. *Proc. Natl Acad. Sci. USA* **34**, 565–581.
18. Metz J, Liancourt P, Kigel J, Harel D, Sternberg M, Tielbörger K. 2010 Plant survival in relation to seed size along environmental gradients: a long-term study from semi-arid and Mediterranean annual plant communities. *J. Ecol.* **98**, 697–704. (doi:10.1111/j.1365-2745.2010.01652.x)
19. Adler PB, Fajardo A, Kleinhesselink AR, Kraft NJB. 2013 Trait-based tests of coexistence mechanisms. *Ecol. Lett.* **16**, 1294–1306. (doi:10.1111/ele.12157)
20. Díaz S *et al.* 2016 The global spectrum of plant form and function. *Nature* **529**, 167–171. (doi:10.1038/nature16489)
21. Grime J. 1977 Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* **111**, 1169–1194. (doi:10.1086/283244)
22. Villa Martin P, Hidalgo J, Rubio de Casas R, Muñoz MA. 2016 Eco-evolutionary model of rapid phenotypic diversification in species-rich communities. *PLoS Comput. Biol.* **12**, e1005139. (doi:10.1371/journal.pcbi.1005139)
23. Falster DS, Brännström Å, Westoby M, Dieckmann U. 2017 Multitrait successional forest dynamics enable diverse competitive coexistence. *Proc. Natl Acad. Sci. USA* **114**, E2719–E2728. (doi:10.1073/pnas.1610206114)
24. Mayfield MM, Bonser SP, Morgan JW, Aubin I, McNamara S, Vesk PA. 2010 What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Glob. Ecol. Biogeogr.* **19**, 423–431.
25. Wright IJ *et al.* 2004 The worldwide leaf economics spectrum. *Nature* **428**, 821–827. (doi:10.1038/nature02403)
26. Westoby M. 1998 A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* **199**, 213–227. (doi:10.1023/A:1004327224729)
27. de Bello F *et al.* 2021 Functional trait effects on ecosystem stability: assembling the jigsaw puzzle. *Trends Ecol. Evol.* **36**, 822–836. (doi:10.1016/j.tree.2021.05.001)
28. Reich PB. 2014 The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *J. Ecol.* **102**, 275–301. (doi:10.1111/1365-2745.12211)
29. Grime JP. 2001 *Plant strategies. Vegetation processes, and ecosystem properties*. New York, NY: John Wiley and sons.
30. Kraft NJB, Crutsinger GM, Forrestel EJ, Emery NC. 2014 Functional trait differences and the outcome of community assembly: an experimental test with vernal pool annual plants. *Oikos* **123**, 1391–1399. (doi:10.1111/oik.01311)
31. Laughlin DC. 2014 The intrinsic dimensionality of plant traits and its relevance to community assembly. *J. Ecol.* **102**, 186–193. (doi:10.1111/1365-2745.12187)
32. Adler PB, HilleRisLambers J, Kyriakidis PC, Guan Q, Levine JM. 2006 Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proc. Natl Acad. Sci. USA* **103**, 12 793–12 798. (doi:10.1073/pnas.0600599103)
33. Craven D *et al.* 2018 Multiple facets of biodiversity drive the diversity – stability relationship. *Nat. Ecol. Evol.* **2**, 1579–1587. (doi:10.1038/s41559-018-0647-7)
34. Polley HW, Isbell FI, Wilsey BJ. 2013 Plant functional traits improve diversity-based predictions of temporal stability of grassland productivity. *Oikos* **122**, 1275–1282. (doi:10.1111/j.1600-0706.2013.00338.x)
35. Chollet S, Rambal S, Fayolle A, Hubert D, Foulquié D, Garnier E. 2014 Combined effects of climate, resource availability, and plant traits on biomass produced in a Mediterranean rangeland. *Ecology* **95**, 737–748. (doi:10.1890/13-0751.1)
36. Sperandii MG *et al.* 2022 LOTVS: a global collection of permanent vegetation plots. *J. Veg. Sci.* **33**, e13115. (doi:10.1111/jvs.13115)
37. Valencia E *et al.* 2020a Synchrony matters more than species richness in plant community stability at a global scale. *Proc. Natl Acad. Sci. USA* **117**, 24 345–24 351. (doi:10.1073/pnas.1920405117)
38. Valencia E *et al.* 2020b Directional trends in species composition over time can lead to a widespread overemphasis of year-to-year asynchrony. *J. Veg. Sci.* **31**, 792–802.
39. Kattge J *et al.* 2020 TRY plant trait database—enhanced coverage and open access. *Glob. Change Biol.* **26**, 119–188. (doi:10.1111/gcb.14904)
40. Garnier E *et al.* 2017 Towards a thesaurus of plant characteristics: an ecological contribution. *J. Ecol.* **105**, 298–309. (doi:10.1111/1365-2745.12698)
41. Cayuela L, Stein A, Oksanen J. 2017 *Taxonstand: taxonomic standardization of plant species names*. R package version 2.0. R Foundation for Statistical Computing. See https://CRAN.R-project.org/package=Taxonstand.
42. Bates D, Mächler M, Bolker B, Walker S. 2014 *Fitting linear mixed-effects models using lme4*. R package version 1.1. R Foundation for Statistical Computing. See https://CRAN.R-project.org/package=lme4.
43. Nakagawa S, Schielzeth H. 2013 A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142. (doi:10.1111/j.2041-210x.2012.00261.x)
44. Nakagawa S, Johnson PCD, Schielzeth H. 2017 The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J. R. Soc. Interface* **14**, 20170213. (doi:10.1098/rsif.2017.0213)
45. de Bello F, Šmilauer P, Diniz-Filho JAF, Carmona CP, Lososová Z, Herben T, Götzenberger L. 2017 Decoupling phylogenetic and functional diversity to reveal hidden signals in community assembly. *Methods Ecol. Evol.* **8**, 1200–1211. (doi:10.1111/2041-210X.12735)
46. Turnbull LA, Rees M, Crawley MJ. 1999 Seed mass and the competition/colonization trade-off: a sowing experiment. *J. Ecol.* **87**, 899–912. (doi:10.1046/j.1365-2745.1999.00405.x)
47. Pistón N, de Bello F, Dias AT, Götzenberger L, Rosado BH, de Mattos EA, Salguero-Gómez R, Carmona CP. 2019 Multidimensional ecological analyses demonstrate how interactions between functional traits shape fitness and life history strategies. *J. Ecol.* **107**, 2317–2328. (doi:10.1111/1365-2745.13190)
48. Kazakou E, Vile D, Shipley B, Gallet C, Garnier E. 2006 Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Funct. Ecol.* **20**, 21–30. (doi:10.1111/j.1365-2435.2006.01080.x)
49. Smart SM *et al.* 2017 Leaf dry matter content is better at predicting above-ground net primary production than specific leaf area. *Funct. Ecol.* **31**, 1336–1344. (doi:10.1111/1365-2435.12832)
50. Thompson K, Band SR, Hodgson JG. 1993 Seed size and shape predict persistence in soil. *Funct. Ecol.* **7**, 236. (doi:10.2307/2389893)
51. Moles AT, Westoby M. 2006 Seed size and plant strategy across the whole life cycle. *Oikos* **113**, 91–105. (doi:10.1111/j.0030-1299.2006.14194.x)
52. Venable DL, Brown JS. 1988 The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.* **131**, 360–384. (doi:10.1086/284795)
53. Pake CE, Venable DL. 1995 Is coexistence of Sonoran desert annuals mediated by temporal variability reproductive success? *Ecology* **76**, 246–261. (doi:10.2307/1940646)
54. Lepš J. 2004 Variability in population and community biomass in a grassland community affected by environmental productivity and diversity. *Oikos* **107**, 64–71. (doi:10.1111/j.0030-1299.2004.13023.x)
55. Conti L *et al.* 2023 Functional traits trade-offs define plant population stability worldwide [Data set]. Zenodo. (doi:10.5281/zenodo.7978254)
56. Conti L *et al.* 2023 Functional trait trade-offs define plant population stability across different biomes. Figshare. (doi:10.6084/m9.figshare.c.6688799)