

Late Quaternary climate legacies in contemporary plant functional composition

Article

Accepted Version

Blonder, B., Enquist, B. J., Graae, B. J., Kattge, J., Maitner, B. S., Morueta-Holme, N., Ordonez, A., Šímová, I., Singarayer, J., Svenning, J.-C., Valdes, P. J. and Violle, C. (2018) Late Quaternary climate legacies in contemporary plant functional composition. *Global Change Biology*, 24 (10). pp. 4827-4840. ISSN 1365-2486 doi: <https://doi.org/10.1111/gcb.14375>
Available at <http://centaur.reading.ac.uk/78204/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1111/gcb.14375>

Publisher: Wiley-Blackwell

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online



Late Quaternary climate legacies in contemporary plant functional composition

Journal:	<i>Global Change Biology</i>
Manuscript ID	GCB-18-0470.R1
Wiley - Manuscript type:	Primary Research Articles
Date Submitted by the Author:	n/a
Complete List of Authors:	Blonder, Benjamin; Arizona State University, School of Life Sciences Enquist, Brian; University of Arizona, Ecology and Evolutionary Biology Graae, Bente; Norwegian University of Science and Technology, Department of Biology Kattge, Jens; Max-Planck-Institute for Biogeochemistry, Organismic Biogeochemistry Maitner, Brian; University of Arizona, Ecology and Evolutionary Biology Morueta-Holme, Naia; University of Copenhagen Ordonez, Alejandro Simova, Irena; Charles University Singarayer, Joy; University of Reading Svenning, Jens-Christian; Aarhus University, Department of Bioscience - Ecoinformatics and Biodiversity Valdes, Paul; University of Bristol, School of Geographical Sciences Violle, Cyrille; CNRS, Centre d'Ecologie Fonctionnelle et Evolutive
Keywords:	functional diversity, functional trait, disequilibrium, lag, climate change, legacy, immigration, exclusion
Abstract:	The functional composition of plant communities is commonly thought to be determined by contemporary climate. However, if rates of climate-driven immigration and/or exclusion of species are slow, then contemporary functional composition may be explained by paleoclimate as well as by contemporary climate. We tested this idea by coupling contemporary maps of plant functional trait composition across North and South America to paleoclimate means and temporal variation in temperature and precipitation from the Last Interglacial (120 ka) to the present. Paleoclimate predictors strongly improved prediction of contemporary functional composition compared to contemporary climate predictors, with a stronger influence of temperature in North America (especially during periods of ice melting) and of precipitation in South America (across all times). Thus, climate from tens of thousands of years ago influences contemporary functional composition via slow assemblage dynamics.

SCHOLARONE™
Manuscripts

For Review Only

1 **Title**

2 Late Quaternary climate legacies in contemporary plant functional composition

3

4 **Running head**

5 Climate legacies in functional composition

6

7 **Authors**

8 Benjamin Blonder^{1,2,3*}

9 Brian J. Enquist^{4,5}

10 Bente J. Graae²

11 Jens Kattge^{6,7}

12 Brian S. Maitner⁴

13 Naia Morueta-Holme⁸

14 Alejandro Ordóñez^{9,10}

15 Irena Simova^{11,12}

16 Joy Singarayer¹³

17 Jens-Christian Svenning^{9,14}

18 Paul J Valdes¹⁵

19 Cyrille Violle¹⁶

20

21 **Affiliations**

22 1: Environmental Change Institute, School of Geography and the Environment, University of

23 Oxford, Oxford, United Kingdom

- 24 2: Department of Biology, Norwegian University of Science and Technology, Trondheim,
25 Norway
- 26 3: School of Life Sciences, Arizona State University, Tempe, Arizona, USA
- 27 4: Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona,
28 United States
- 29 5: Santa Fe Institute, Santa Fe, New Mexico, United States
- 30 6: Max Planck Institute for Biogeochemistry, Jena, Germany
- 31 7: German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Germany
- 32 8: Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark,
33 University of Copenhagen, Copenhagen, Denmark
- 34 9: Section for Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University,
35 Aarhus C, Denmark
- 36 10: School of Biological Sciences, Queens University, Belfast, Northern Ireland
- 37 11: Center for Theoretical Study, Charles University, Prague, Czech Republic
- 38 12: Department of Ecology, Faculty of Science, Charles University, Prague, Czech Republic
- 39 13: Department of Meteorology, University of Reading, Reading, United Kingdom
- 40 14: Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Aarhus University,
41 Aarhus, Denmark
- 42 15: School of Geographical Sciences, University of Bristol, Bristol, United Kingdom
- 43 16: CNRS, CEFE, Université de Montpellier – Université Paul Valéry – EPHE, Montpellier,
44 France
- 45
- 46

47 *: Corresponding author, bblonder@gmail.com, +1 480 965 6419, School of Life Sciences,
48 Arizona State University, Tempe, Arizona, USA

49

50 **Key words**

51 Functional diversity, functional trait, disequilibrium, lag, climate change, legacy, immigration,
52 exclusion, Holocene, Pleistocene

53

54 **Submission type**

55 Primary research article

56

57

For Review Only

58 Abstract

59 The functional composition of plant communities is commonly thought to be determined by
60 contemporary climate. However, if rates of climate-driven immigration and/or exclusion of
61 species are slow, then contemporary functional composition may be explained by paleoclimate
62 as well as by contemporary climate. We tested this idea by coupling contemporary maps of plant
63 functional trait composition across North and South America to paleoclimate means and
64 temporal variation in temperature and precipitation from the Last Interglacial (120 ka) to the
65 present. Paleoclimate predictors strongly improved prediction of contemporary functional
66 composition compared to contemporary climate predictors, with a stronger influence of
67 temperature in North America (especially during periods of ice melting) and of precipitation in
68 South America (across all times). Thus, climate from tens of thousands of years ago influences
69 contemporary functional composition via slow assemblage dynamics.

70 **Introduction**

71 Shifts in the functional composition of plant communities can indicate variation in ecosystem
72 functioning and ecosystem services (Chapin *et al.*, 2000, Díaz & Cabido, 2001, Hooper *et al.*,
73 2005, Jetz *et al.*, 2016). Forecasting the two components of functional composition, functional
74 trait means (FM) and functional diversity (FD) (Villéger *et al.*, 2008), is therefore of central
75 interest. Insights into geographic variation in the contemporary functional composition of plant
76 communities (Violle *et al.*, 2014) comes from field surveys (Asner *et al.*, 2014, Baraloto *et al.*,
77 2010, De Bello *et al.*, 2006), macroecological approaches (Campbell & McAndrews, 1993,
78 Lamanna *et al.*, 2014, Šimová *et al.*, 2015, Swenson *et al.*, 2012), and remote sensing approaches
79 (Asner *et al.*, 2017a, Asner *et al.*, 2017b, Jetz *et al.*, 2016). However, little is known about
80 changes in these functional trait patterns over longer time scales (Blonder *et al.*, 2014, Polly *et al.*
81 *et al.*, 2011, Thuiller *et al.*, 2008). There is also growing evidence that paleoclimate has directly
82 and indirectly structured contemporary species composition and functional composition
83 (Ordonez & Svenning, 2016, Svenning *et al.*, 2015). It has been unclear how these paleoclimate
84 effects on species composition translate to differences in functional composition, because even
85 species assemblages in disequilibrium with contemporary climate may have equilibrium
86 functional relationships with contemporary climate (Fukami *et al.*, 2005).

87 A core hypothesis of plant functional ecology is that contemporary environments
88 determine contemporary functional composition (Enquist *et al.*, 2015, Grime, 1974, Raunkiaer,
89 1907, Schimper, 1898, von Humboldt & Bonpland, 1807 (tr. 2009)). Many studies have shown
90 relationships between FMs or FD and contemporary environmental variables, e.g. Cornwell and
91 Ackerly (2009), Moles *et al.* (2014), suggesting equilibrium with contemporary environmental
92 conditions is plausible. However, paleoclimate may also have had a strong influence on

93 contemporary functional composition at large spatial scales (Svenning *et al.*, 2015). A mismatch
94 could exist between contemporary climate and contemporary FMs and FD because of
95 disequilibrium in species' geographic ranges and lack of more appropriate species in the regional
96 pool (Davis & Shaw, 2001, Enquist *et al.*, 2015). Mechanisms that could lead to differing
97 degrees of lagged responses of FMs and FD, and thus disequilibrium, include differential rates of
98 exclusion and immigration driven by variation in dispersal limitation, longevity, and species
99 interaction strengths that are associated with certain functional traits (Davis, 1984, Eiserhardt *et*
100 *al.*, 2015, Enquist *et al.*, 2015, Svenning & Sandel, 2013, Webb, 1986). Evidence for
101 disequilibrium in functional composition is growing. For example, instability in climate in the
102 Late Quaternary may have influenced contemporary functional composition in Europe (Mathieu
103 & Jonathan Davies, 2014, Ordonez & Svenning, 2015, Ordonez & Svenning, 2017, Svenning
104 *et al.*, 2015) and in the Americas (Ordonez & Svenning, 2016).

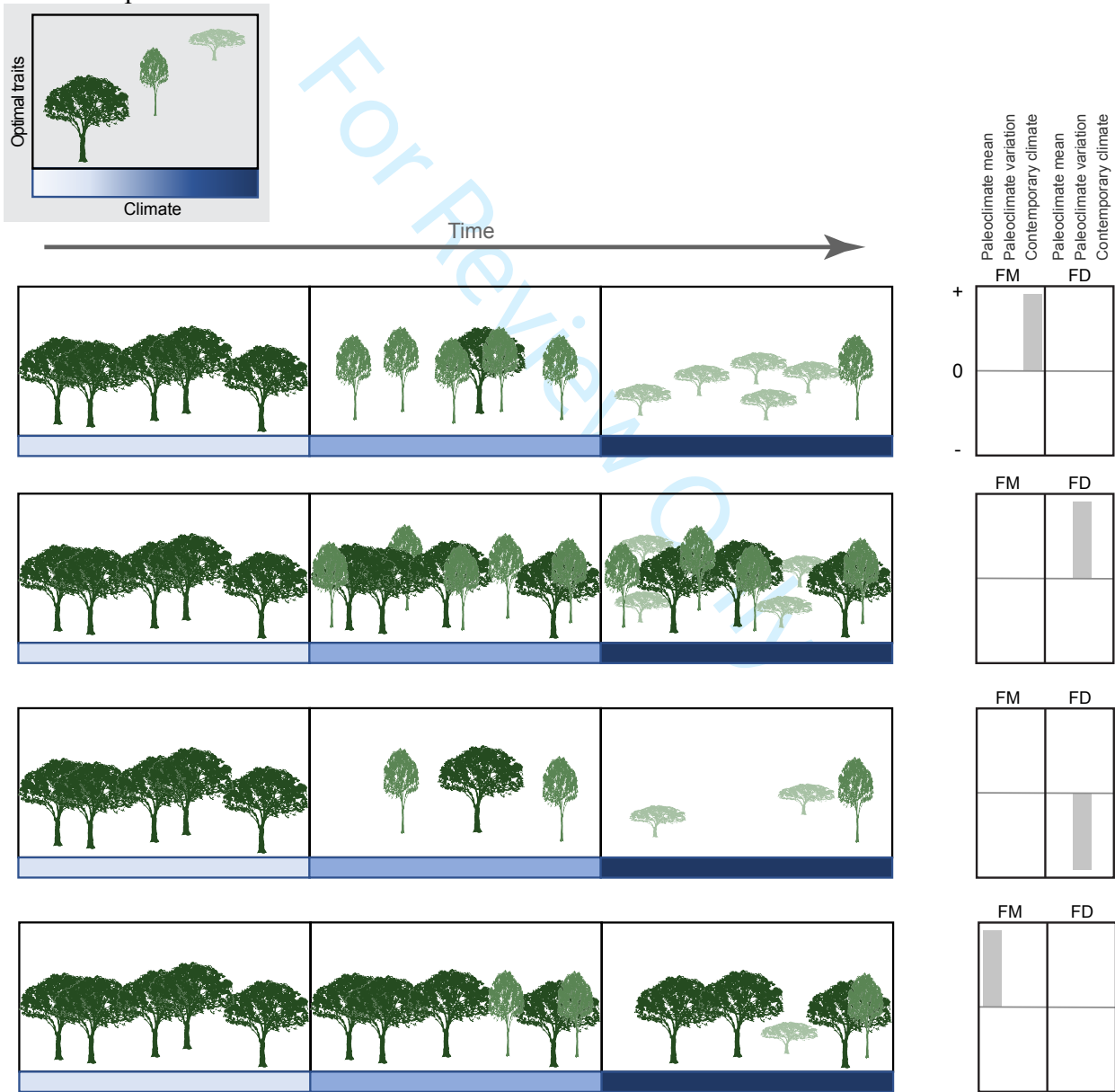
105 Paleoclimate influences on plant species composition are better known. For example,
106 many tropical forests and temperate understory assemblages have compositions lagging
107 contemporary climate changes at 10^1 - 10^3 year timescales (Campbell & McAndrews, 1993, Cole
108 *et al.*, 2014, DeVicor *et al.*, 2008, La Sorte & Jetz, 2012). At 10^3 - 10^5 year timescales, the
109 European flora (Svenning & Skov, 2007) and North American plant range size distributions
110 (Morueta-Holme *et al.*, 2013) show strong signals of slow recovery from cover of ice sheets due
111 to late-Quaternary glaciation. At 10^5 - 10^6 year timescales, African and Madagascan palm
112 distributions can be predicted by Pliocene precipitation patterns (Blach-Overgaard *et al.*, 2013,
113 Rakotoarinivo *et al.*, 2013). Last, at 10^6 - 10^7 year timescales, Cenozoic climate change and land
114 connectivity shifts have resulted in cold tolerance-driven extinction of some temperate trees

115 (Eiserhardt *et al.*, 2015), and have limited the dispersal and radiation of certain clades (Morley,
116 2011, Woodruff, 2010).

117 We first test a hypothesis (Hypothesis 0) that paleoclimate has additional predictive
118 power for functional composition beyond that provided by contemporary climate. We do so by
119 determining whether FMs or FD are best predicted by contemporary climate alone or by
120 contemporary climate and paleoclimate together.

121 We also test four hypotheses for how paleoclimate and contemporary climate could
122 influence contemporary FMs and FD (**Figure 1**). The hypotheses explore fast vs. slow processes
123 for exclusion and immigration of species under linear change in a mean climate value (Blonder
124 *et al.*, 2017). ‘Fast’ and ‘slow’ are terms used to indicate temporal rates of change in species
125 composition and functional traits relative to the rate of climate change; mechanisms underlying
126 exclusion and immigration could include ecological processes such as environmental filtering,
127 competition, or dispersal or evolutionary processes such as speciation, adaptation, or extinction.
128 These hypotheses are thus relevant over intervals where changes in climate can be treated as
129 linear. They also all assume an underlying linear trait-environment relationship that would be
130 obtained in the equilibrium limit.

131 **Figure 1.** Four hypothetical scenarios for the relationship between contemporary functional traits
 132 and climate change. Inset panel shows the assumed equilibrium trait-environment relationship.
 133 **A)** Hypothesis 1, fast exclusion and fast immigration: species will track contemporary climate,
 134 and there will be a strong contemporary climate mean – functional trait mean relationship. **B)**
 135 Hypothesis 2, slow exclusion but fast immigration: many species that were at one time suitable
 136 still remain part of the assemblage, and there will be a positive relationship between paleoclimate
 137 temporal variation and functional diversity. **C)** Hypothesis 3, fast exclusion but slow
 138 immigration: only species that were at all times suitable will be able to enter the assemblage, and
 139 there will be a negative relationship between paleoclimate temporal variation and functional
 140 diversity. **D)** Hypothesis 4, slow exclusion and slow immigration: species will fail to track
 141 contemporary climate, and there will be a strong paleoclimate mean – functional trait mean
 142 relationship.



143

144 In Hypothesis 1 (**Figure 1A**), if exclusion of species with inappropriate traits for a novel
145 climate is fast and if immigration of more appropriate species is fast, then contemporary climate
146 mean – contemporary FM relationships will exist. In Hypothesis 2 (**Figure 1B**), if exclusion of
147 species with inappropriate traits is slow and if immigration of more appropriate species is fast,
148 paleoclimate temporal variation – contemporary FD relationships will be positive because more
149 species with appropriate traits are continually added to the assemblage without loss of other
150 species. In Hypothesis 3 (**Figure 1C**), if exclusion of species with inappropriate traits is fast but
151 if immigration of appropriate species is slow, then paleoclimate temporal variation –
152 contemporary FD relationships will be negative because species with inappropriate traits become
153 lost from an assemblage without replacement by other species. In Hypothesis 4 (**Figure 1D**), if
154 exclusion is slow and if immigration is slow, then paleoclimate mean – contemporary FM
155 relationships will exist because of temporally lagged losses and gains of suitable species.

156 These four hypotheses provide non-exclusive predictions of relationships between
157 climate and functional trait patterns. More than one of these patterns could be simultaneously
158 observed, depending on the dynamics of climate over a long period comprising multiple
159 approximately linear changes. That is, predictions of relationships between e.g. paleoclimate
160 variation and contemporary FD do not preclude observation of relationships between
161 paleoclimate mean and contemporary FMs.

162 Here, we ask: 1) whether paleoclimate means and temporal variation improve predictions
163 of contemporary FMs and FD (Hypothesis 0), and 2) which of the proposed hypotheses
164 (Hypothesis 1 - Hypothesis 4) are consistent with empirical patterns of contemporary FMs and
165 FD. We derived gridded maps of contemporary FMs and FD (as convex hull volume (Cornwell
166 *et al.*, 2006)) across the Americas by merging species-mean trait data with maps of species

167 distributions. We used five plant functional traits that are representative of major ecological
168 strategy axes (Díaz *et al.*, 2016, Westoby & Wright, 2006), and predictive of species sorting
169 along environmental gradients (Moles *et al.*, 2014, Simova *et al.*, 2018, Šímová *et al.*, 2015). We
170 then coupled these estimates with contemporary and paleoclimate maps at timescales spanning
171 the Last Interglacial (120 ka) to the present. We chose climate axes of mean annual temperature
172 and annual precipitation because of their established trait-environment relationships (Moles *et*
173 *al.*, 2014), and their ability to be reconstructed by general circulation models.

174

175 **Materials and Methods**

176 *Species distribution maps*

177 We obtained occurrence data for New World plants from the BIEN database (version 3.0, access
178 date 26 February 2017, <http://www.biendata.org>) (Enquist *et al.*, 2009, Enquist *et al.*, in
179 preparation, Maitner *et al.*, 2017). Following Morueta-Holme *et al.* (2013), we selected only data
180 that represented geo-validated and non-cultivated occurrences, and standardized all taxonomic
181 names (Boyle *et al.*, 2013). Occurrence points were non-randomly distributed, with higher
182 observation densities in the continental United States and in Central America / northwestern
183 South America.

184 To reduce biases from spatial variation in sampling intensity, we estimated species'
185 geographic ranges using convex hulls (Elith & Leathwick, 2009). Convex hulls can be estimated
186 without using climate variables for niche modeling, avoiding any potential circularity in our
187 analyses that would be caused by (for example) a maximum entropy model calibrated on
188 contemporary climate variables. We generated range polygons from latitude/longitude
189 coordinates for species with more than three non-collinear observation points. For species with

190 three or fewer observations (6,886/74,491 species=9.2%), we assumed that the species was
191 present only in the 100×100-km grid cell(s) containing the observation. We rasterized
192 predictions over the Western Hemisphere on a 100×100-km grid cell equal area projection
193 centered at 80°W, 15°N.

194

195 *Functional trait data*

196 We selected five functional traits representing major ecological strategy axes for growth,
197 survival, and reproduction (Díaz *et al.*, 2016, Westoby & Wright, 2006). These included specific
198 leaf area, plant height, seed mass, stem specific density, and leaf nitrogen. Trait data were
199 obtained from the TRY database (<https://www.try-db.org>, accession date 19 June 2013) (Kattge
200 *et al.*, 2011), covering 45,507 species (7,051 genera). A list of data references is in **Table S1**.
201 Because many taxa were missing some observations of certain variables, a phylogenetic gap-
202 filling approach (Schrodt *et al.*, 2015) was used to estimate missing values; then for a fraction of
203 taxa that were present in the occurrence data but not present in the TRY data (59,423 species,
204 3343 genera), missing values were filled with genus means estimated from the TRY data. This
205 approach likely results in less bias than omitting data for species without exact matches to trait
206 data.

207 We also categorized each species by its growth habit. Using a New World database
208 (Engemann *et al.*, 2016), we classified species as woody (29,676 species) or non-woody (44,324
209 species). Analyses were carried out for either all or only woody species to distinguish potentially
210 different climate drivers on traits between growth forms (Díaz *et al.*, 2016, Simova *et al.*, 2018).

211

212 *Functional trait mapping*

213 We used the distribution maps to estimate the species composition within each grid cell. We then
214 matched this species list against the functional trait data to estimate the distribution of log-
215 transformed traits within each grid cell. To reduce undersampling biases, we then removed from
216 the analysis all cells with richness of species with non-missing trait values less than 100 (a value
217 chosen to be small, in this case representing the 7% quantile of the data, and which primarily
218 removes extreme-latitude cells in Greenland and Ellesmere Island in the northern hemisphere,
219 and Tierra del Fuego in the southern hemisphere) (**Figure S1**). This procedure was repeated for
220 woody species and for all species.

221 To estimate FMs, we calculated the average trait value across all species occurring within
222 the cell, based on overlapping range maps. To simplify these five axes, we calculated a ‘FM
223 PC1’, defined as the score along the first principal component of the five mapped trait axes. This
224 axis explained 83.5% of the variation in traits for the woody species subset and 74.5% of the
225 variation for all species, and corresponds to increasing plant height, seed mass, and stem specific
226 density, as well as decreasing SLA and leaf nitrogen content (**Figure S2**).

227 To estimate FD, we first calculated the five-dimensional convex hull volume across log-
228 transformed values of each trait value occurring within the cell (Villéger *et al.*, 2008). Second,
229 we corrected this estimate because convex hull volumes often scale linearly with sample size,
230 and because the fraction of species per grid cell with available trait measurements (‘trait
231 coverage’) was variable (78% mean, 10% s.d). This value was sufficiently high to lead to limited
232 bias in FM estimates, according to simulations (Borgy *et al.*, 2017c). To correct for the sample
233 size effect in FD, we built a null model. We calculated the convex hull volume of random
234 samples of the full trait dataset with species richness varying from 100 to 10,000 in steps of 100
235 (‘FD_{true}’), then subsampled each to a trait coverage value varying from 0.05 to 1.0 in steps of

236 0.05, and then recalculated the convex hull volume based on this subsample ('FD_{observed}'). We
237 repeated the convex hull volume calculation 10 times for each combination of species richness
238 and trait coverage. We then built a linear model to predict FD_{true} on the basis of linear terms of
239 FD_{observed}, species richness, and trait coverage, as well as 2-way and 3-way interactions between
240 these variables. This model explained 95.8% of the variation in FD_{true}. We therefore applied this
241 model to FD_{observed} in the empirical data to yield a corrected estimate of FD_{true} (hereafter, FD)
242 that accounted for variation in trait coverage.

243 FD_{observed} and species richness are positively correlated, because as species richness
244 increases within a grid cell, FD_{observed} can only stay constant or increase. Thus, it may be difficult
245 to separate effects of paleoclimate-related processes on FD from effects on species richness. To
246 partially address this issue, we also repeat all analyses for another composite variable FD_{res},
247 defined as the residuals of a regression of the corrected estimate of FD (FD_{true}) on species
248 richness. Thus positive values of FD_{res} indicate FD values higher than expected based on a
249 random assemblage with the same species richness, while negative values indicate values lower
250 than expected.

251

252 *Contemporary climate data*

253 We obtained contemporary climate predictions (1979-2013 AD averages) for mean annual
254 temperature (MAT) and mean annual precipitation (MAP) from the CHELSA dataset version 1.2
255 (available at <http://chelsa-climate.org/>) (Karger *et al.*, 2016). The climate dataset is based on a
256 quasi-mechanistic statistical downscaling of the ERA (European Re-Analysis) interim global
257 circulation model with a GPCC (Global Precipitation Climatology Centre) bias correction, and
258 incorporating topoclimate (Karger *et al.*, 2016). This approach avoids biases inherent to

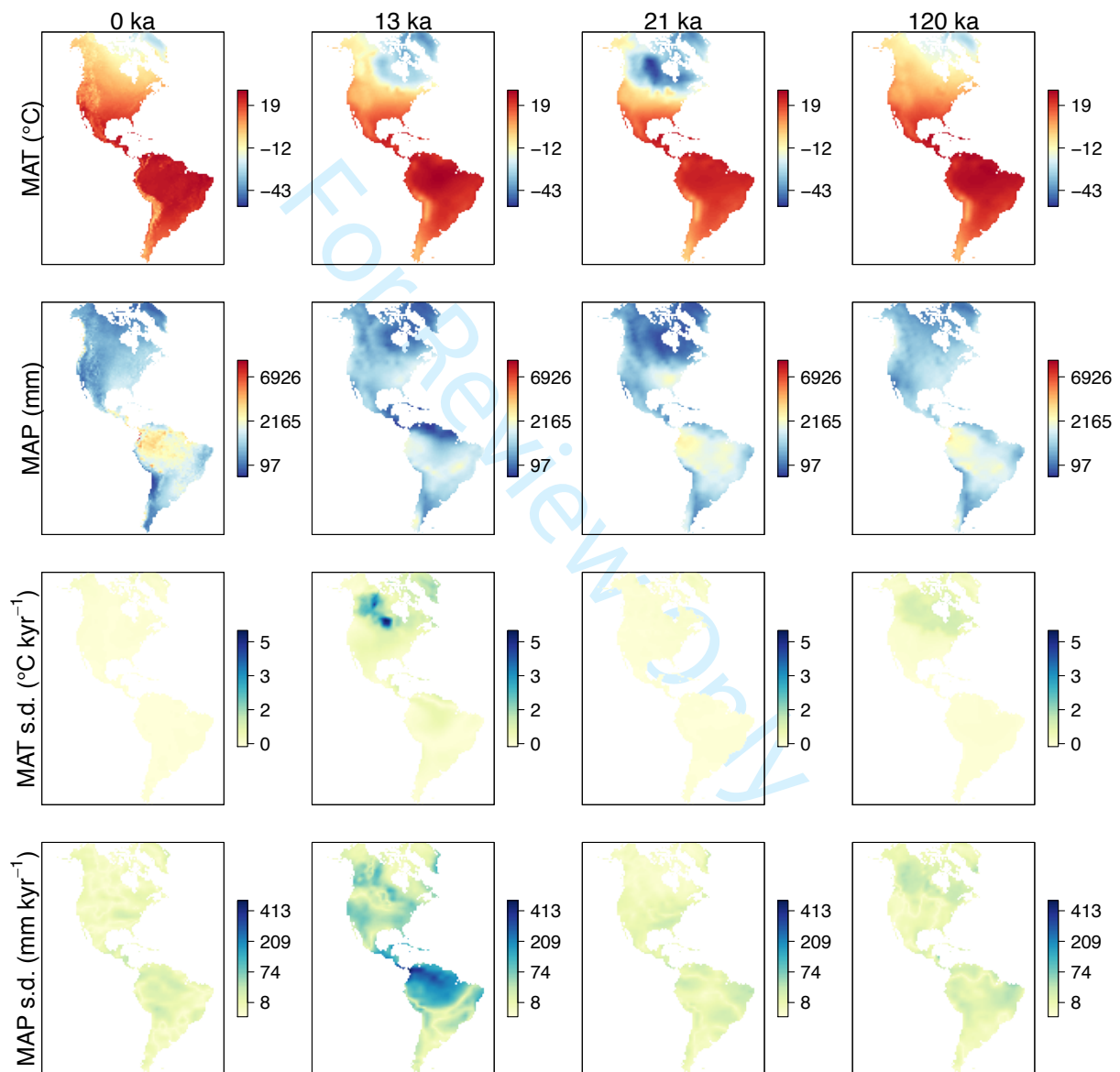
259 interpolation between weather stations with uneven coverage of geographic and climate space.
260 We then re-projected the 1-arcsecond resolution data to the same grid as the species distribution
261 maps.

262

263 *Paleoclimate data*

264 We obtained paleoclimate data from the HadCM3 general circulation model. The HadCM3
265 model consists of a coupled atmospheric, ocean, and sea ice model with non-interactive
266 vegetation, with an atmospheric resolution of 2.5° latitude × 3.75° longitude. The model was
267 driven by variations in orbital configuration, greenhouse gases, ice-sheet topography, and
268 coincident sea level changes and bathymetry since 120 ka. Simulations included the effects of
269 abrupt “fresh-water” pulses and the resulting abrupt climate changes that occurred during at 17
270 ka (Heinrich event) and 13 ka (Younger Dryas). Boundary conditions and spin-up are fully
271 described in Hoogakker *et al.* (2016), Singarayer and Valdes (2010). Data were available at time
272 points beginning 0-120 ka in 1 kyr slices from 1–22 ka, in 2 kyr slices from 22–84 ka, and in 4
273 kyr slices from 84–120 ka (example time slices in **Figure 2**, all time slices in **Figure S3, S4**).
274

275 **Figure 2.** Example contemporary climate and HadCM3 general circulation model temporal mean
 276 values for annual temperature (MAT) and annual precipitation (MAP) as well as for temporal
 277 standard deviations of MAT and MAP for the present day (0 ka), and for intervals beginning at
 278 13 ka (Younger Dryas), 21 ka (Last Glacial Maximum), and 120 ka (Last Interglacial). Colors
 279 are scaled and transformed (see **Materials and Methods**), with labels indicating values back-
 280 transformed to original units. The full analysis includes a larger number of temporal mean values
 281 at intervals spaced between 0 – 120 ka.



282

283 Model output was re-projected to the same coordinate system and resolution as the
284 contemporary species distribution maps. This approach assumes a negligible impact of variation
285 in sea level on the vast majority of pixels and is appropriate given that only contemporary
286 functional composition data were available. Paleoclimate maps are close to contemporary
287 climate maps during the Holocene, and diverge strongly during the Pleistocene, as measured by
288 mean absolute deviation between contemporary and paleoclimate pixel values (**Figure S5**).

289

290 *Statistical analysis*

291 To prepare climate data for analysis, we first square-root transformed contemporary and
292 paleoclimate MAP data to improve normality. We calculated a temporal mean value at x ka, for x
293 in 0 to 120, as well as a temporal standard deviation at x ka within each grid cell using a moving
294 window approach, i.e. over values within the interval $[x-k, x+k]$. These temporal standard
295 deviations were then standardized by divided by the total temporal range of the moving window.
296 Temporal standard deviations thus have units of either $^{\circ}\text{C kyr}^{-1}$ or mm kyr^{-1} . We used a value of
297 $k=1$ where possible, but $k=4$ in some cases where HadCM3 data had coarser resolution (i.e.
298 closer to 120 ka). Edge cases at 0 and 120 ka were calculated treating out-of-range data as
299 missing. Contemporary climate was used for values at 0 ka, while paleoclimate was used for
300 values at 1-120 ka.

301 We then rescaled all contemporary and paleoclimate predictor variables by z -
302 transforming each relative to their grand mean and standard deviation (over all pixels and years)
303 for each variable type from the HadCM3 model (MAT and MAP mean values and temporal
304 standard deviation of MAT and MAP). This approach standardizes values across both variable
305 types and models relative to estimates of their ranges across study interval. Thus, a value of +1 in

306 a MAT layer indicates that this cell has a value that is 1 standard deviation larger than the mean
307 value relative to all values seen in all locations over the 0-120 ka interval.

308 We used partial least squares (PLS) regression to determine the best predictors of FMs,
309 FD, and FD_{res} in independent analyses. We conducted PLS regressions separately for North
310 America and South America (split at the Panama/Colombia border) because of their different
311 glaciation histories (Ehlers *et al.*, 2011). The PLS approach accounts for the statistical non-
312 independence of large numbers of predictors by finding the rotation of the predictor matrix that
313 best overlaps with the response vector, and identifies the latent factors (components) that
314 correspond to these rotations (Geladi & Kowalski, 1986). The PLS components describe the
315 independent contribution of each predictor variable to the response variable and are ordered by
316 their explanatory capacity such that the first component (PLS1) by definition explains the most
317 variation in the data. Thus the approach can identify independent effects of multiple correlated
318 predictors (i.e. separating the effects of contemporary and paleoclimate, even if they are
319 sometimes correlated with each other). We built models that simultaneously incorporated up to
320 six classes of predictors: contemporary climate mean values, paleoclimate temporal mean values,
321 and paleoclimate temporal standard deviations (metrics of paleoclimate variation) for each of
322 MAT and MAP.

323 We also performed a separate set of PLS analyses in order to assess biases from climate
324 changes occurring at times and locations where plants could not have grown. Although
325 predicting ice sheet spatial coverage at each time and location would be ideal, we instead masked
326 out pixels at all times and places where there was ice cover during the Last Glacial Maximum
327 (21 ka) (corresponding to pixels in the black polygon in **Figure 2I**). This choice was motivated

328 by the currently limited knowledge of temporally-resolved ice sheet dynamics during the full
329 extent of study period (Kleman *et al.*, 2013, Kleman *et al.*, 2010).

330 We tested Hypothesis 0 for each of FMs, FD, or FD_{res} by comparing root mean square
331 error of prediction (RMSEP) values for PLS models that included contemporary climate ($n=2$
332 total predictors) and/or paleoclimate values ($n=250$ total predictors). Because RMSEP
333 necessarily decreases with number of PLS components, we compared RMSEP values after fixing
334 the number of PLS components in each model. This approach is more appropriate than model
335 selection methods based on Akaike Information Criterion comparisons (Li *et al.*, 2002) because
336 it is difficult to calculate degrees of freedom in PLS in order to correctly penalize likelihood
337 values (Krämer & Sugiyama, 2011).

338 In this PLS framework, Hypotheses 1–4 can be distinguished by regression of
339 contemporary FMs, FD, or FD_{res} on contemporary climate mean values, paleoclimate mean
340 values over multiple times, and paleoclimate temporal variation over multiple times. We
341 assessed the importance of each PLS component via the percentage of variance explained by the
342 component. The effect of each variable at each time for FMs, FD, or FD_{res} can be interpreted as
343 the PLS component's loading coefficient explaining the most variance in each model, with
344 positive loading coefficients indicating that higher than average (over the 0-120 ka interval)
345 values of this predictor yield higher than average values of the response variable. We also
346 defined an overall effect for each class of predictor as the maximum absolute loading coefficient
347 for that predictor type along each axis across all times.

348 All analyses were carried out with the R statistical environment (version 3.3.3).
349 Occurrence data were obtained with the 'BIEN' package (Maitner *et al.*, 2017). Map rescaling
350 and re-projection were carried out with the 'raster' (Hijmans & van Etten, 2014) and 'maptools'

351 (Bivand & Lewin-Koh, 2013) packages. Convex hulls were calculated with the ‘geometry’
 352 package (Habel *et al.*, 2015). PLS regression was carried out within the ‘pls’ package (Mevik &
 353 Wehrens, 2007).

354

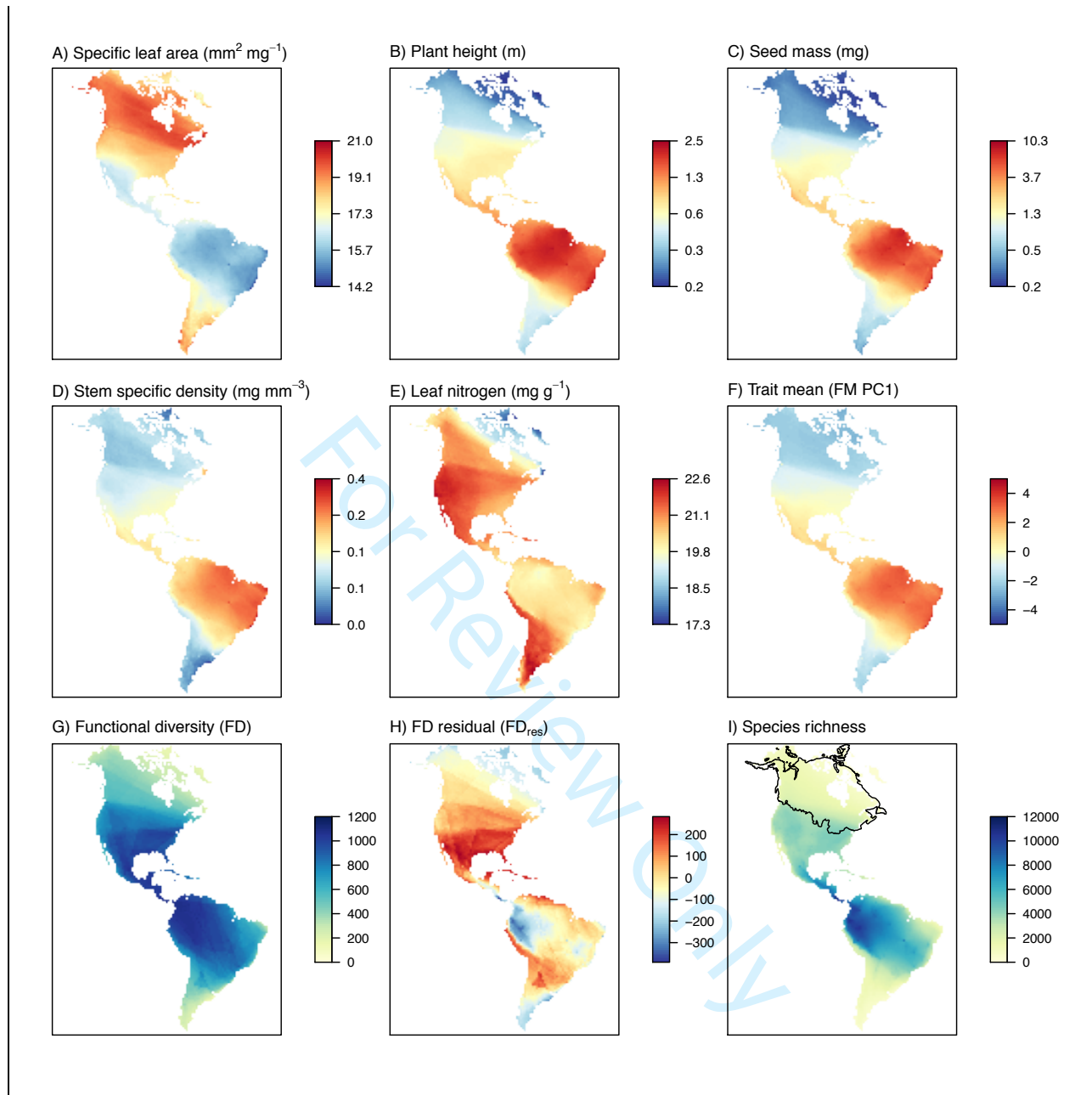
355 **Results**

356 *Contemporary functional trait patterns*

357 Mapped FMs for all species for the five focal functional traits showed strong spatial gradients.
 358 Mean estimates of specific leaf area were highest in temperate/boreal North America (**Figure**
 359 **3A**). Maximum plant height and seed mass were highest in the eastern Amazon basin (**Figure**
 360 **3B, 3C**). Stem specific density was highest in the Amazon basin (**Figure 3D**). Leaf nitrogen
 361 content was highest in western North America and the southern South America (**Figure 3E**), all
 362 leading to similar latitudinal tropical-temperate-boreal gradients in FMs for PC1 (**Figure 3F**).
 363 FD was high throughout the tropics and into southeastern North America (**Figure 3G**), and FD_{res}
 364 was high in southeastern North America, Central America, and the Caribbean, as well as along
 365 the northeastern and eastern coasts of South America (**Figure 3H**). Species richness was highest
 366 in Central America and the western Amazon basin (**Figure 3I**). All of these results were
 367 qualitatively consistent when restricted to woody species only (**Figure S6**).

368

369 **Figure 3.** Estimated plant species assemblage characteristics, based on data for all species.
 370 Distributions of functional trait means (FMs) for five functional traits (each colored by log-
 371 transformed values, with labels indicating values back-transformed to original units) are shown
 372 for **A**) Specific leaf area, **B**) plant height, **C**) seed mass, **D**) stem specific density, and **E**) leaf
 373 nitrogen per unit mass. **F**) First principal component of FMs. **G**) Functional diversity (FD;
 374 convex hull volume of \log_e -transformed values); **H**) FD_{res} , the residual of FD regressed on
 375 species richness, and **I**) Species richness. The black polygon indicates the maximum ice sheet
 376 extent during the Last Glacial Maximum.



377

378

379 *Overall predictive power of paleoclimate*

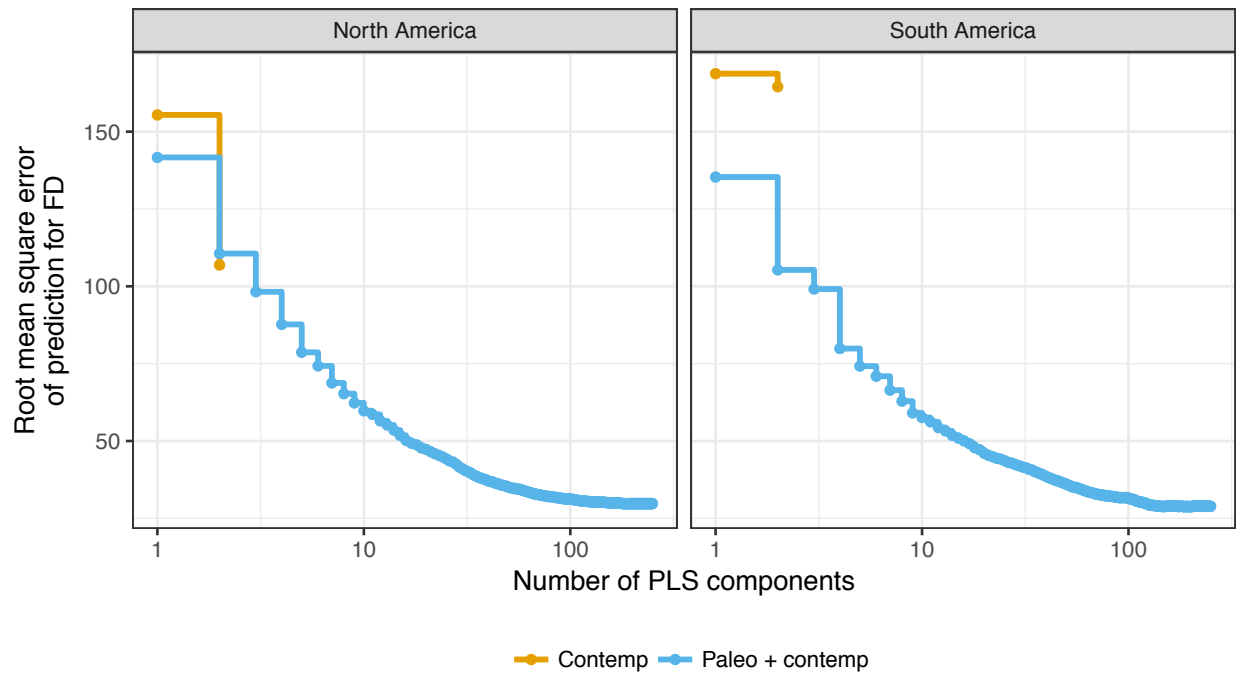
380 We found that models that incorporated paleoclimate and contemporary climate had higher
 381 predictive power than models that incorporated only contemporary climate (**Figure 4**). When
 382 comparing models with the same number of PLS components, the contemporary + paleoclimate
 383 models usually had equivalent or lower root mean square error of prediction (RMSEP) than the

384 contemporary climate models. For example, for FD calculated with data for all species and
385 HadCM3 climate data, using 1 PLS component, RSMEP was 9% lower in North America and
386 20% lower in South America; when using data for woody species, RMSEP was 14% lower in
387 North America and 20% lower in South America. Similar results held for all other response
388 variables, other methodological choices, and 2 PLS components (**Figure S7**).

389

For Review Only

390 **Figure 4.** Predictive uncertainty in models for FD as measured by the cross-validated root mean
 391 squared error of prediction (RMSEP) for increasing numbers of PLS components. Y-axis units
 392 correspond to units of functional diversity (compare to **Figure 3G**). Results are for PLS
 393 regression models generated using trait data for all species and climate data from HadCM3.
 394 Orange lines indicate models using only contemporary climate predictors; blue lines, models
 395 using contemporary and paleoclimate predictors.
 396



397
 398

399 *Paleoclimate and contemporary climate predictors of contemporary functional composition*

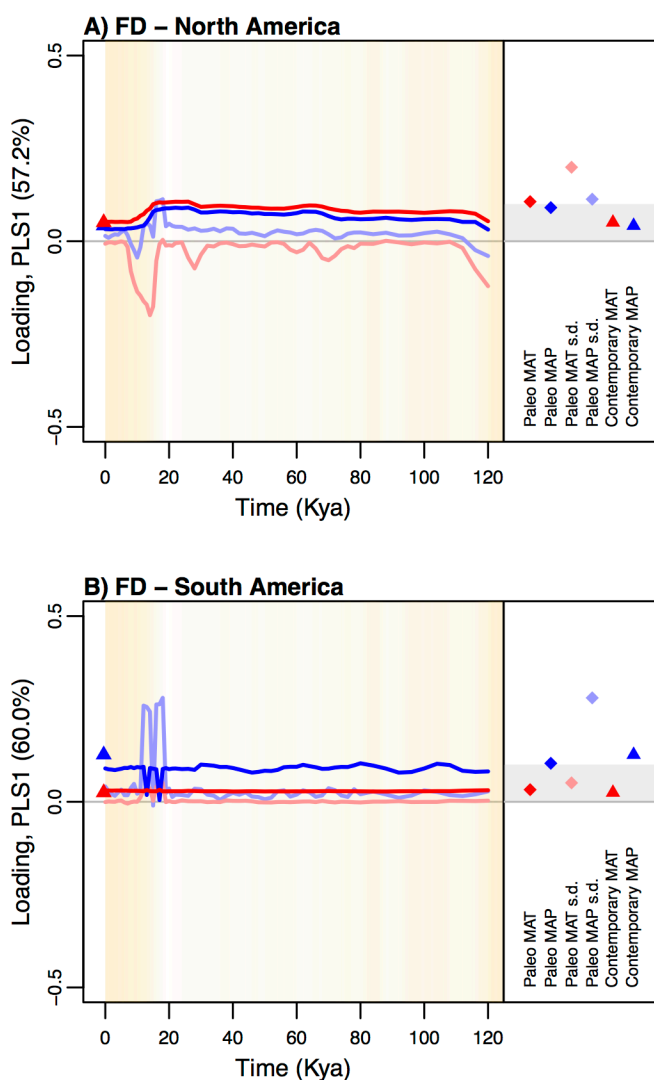
400 We present results for the HadCM3 paleoclimate model using all species, as results are
401 representative across all modeling choices.

402 For FD in North America, we found that the first PLS component explained 57% of the
403 variation in the data (**Figure 5A**). This component represented large effects (> 0.1 in absolute
404 standard deviations) for paleo MAT mean value (+0.11), paleo MAT temporal standard deviation
405 (-0.20), and for paleo MAP temporal standard deviation (+0.11). There were no large effects
406 from contemporary MAT or MAP mean values. These effects were strongest immediately after
407 the Last Glacial Maximum (~20 ka) and the Last Interglacial (~120 ka).

408 For FD in South America, we found that the first PLS component explained 60% of the
409 variation in the data (**Figure 5B**). This component represented large effects for contemporary
410 MAP mean value (+0.13), paleo MAP mean value (+0.10), and paleo MAP temporal standard
411 deviation (+0.28). There was no large effect from any MAT predictor. Paleo MAP temporal
412 standard deviation was most important at time periods beginning at 17 ka and 13 ka,
413 corresponding to abrupt change from a Heinrich event and the Younger Dryas, respectively.

414

415 **Figure 5.** Contemporary climate and paleoclimate effects on functional diversity (FD), for the
 416 first PLS component, for **A) North America**, and **B) South America**. Results are for models
 417 generated using trait data for all species and using climate data from HadCM3. Left subpanels
 418 indicate effect sizes (loading coefficients) for each model component at different times.
 419 Contemporary climate data are shown in triangles; paleoclimate values as dark lines and
 420 temporal standard deviations as lighter lines. Red indicates MAT, blue MAP. Right subpanel
 421 symbols indicate the maximum absolute effect for each variable class over time. A gray
 422 background rectangle indicates a significance threshold. Orange shading behind each panel
 423 indicates global atmospheric temperatures reconstructed by Bintanja *et al.* (2011), with deeper
 424 shading indicating warmer conditions. Results for FMs and FD_{res} are shown in **Figure S8**.



425

426

427 Results for FMs and FD_{res} were similar to those for FD. One exception occurred in South
428 America, where estimates for FD_{res} were opposite in sign (**Figure S8**). Results for higher PLS
429 components are not reported, as explained variation for each was individually low (e.g. at most 7
430 - 13% for PLS2 across all response variables using the HadCM3 data and all species across
431 response variables). Model residuals for North and South America for varying numbers of
432 components are shown in **Figure S9**.

433 All of the above results were qualitatively similar when restricting data to woody-only
434 species (**Figure S10**). Analyses were also qualitatively similar when excluding pixels covered by
435 ice sheets at the Last Glacial Maximum. Results for these analyses are presented in **Figure S11**.

437 **Discussion**

438 We identified spatially and temporally variable effects of paleoclimate on contemporary
439 functional trait patterns, independent from those of contemporary climate. Across
440 methodological choices, functional composition was predicted in North America by paleo MAT
441 mean values, paleo MAT temporal standard deviations, and paleo MAP temporal standard
442 deviation, and in South America by paleo MAP mean values and paleo MAP mean values. Paleo
443 MAT and MAP mean values had similar effects over time, while in North America MAT
444 temporal standard deviation at the Last Glacial Maximum and Last Interglacial had strongest
445 effects, and in South America MAP temporal standard deviation at the Younger Dryas and the 17
446 ka Heinrich event had strongest effects. Thus climate immediately after the Last Glacial
447 Maximum appears to have left a strong legacy on contemporary functional composition. We also
448 found that paleoclimate was a useful predictor of contemporary functional composition,
449 supporting Hypothesis 0. Predictive errors for predicting FMs, FD, and FD_{res} were lower when

450 paleoclimate variables were incorporated into regression models than when only including
451 contemporary climate variables.

452 The PLS models support several of the hypotheses. Hypothesis 1 (a relationship between
453 contemporary FMs and contemporary climate mean values, with fast immigration and fast
454 exclusion) was supported in South America for MAP. Hypothesis 2 (a positive relationship
455 between contemporary FD and paleoclimate temporal standard deviation, with fast immigration
456 slow exclusion) was supported for MAP in North America and in South America. Hypothesis 3
457 (a negative relationship between contemporary FD and paleoclimate temporal standard
458 deviation, with slow immigration and fast exclusion) was supported for MAT in North America.
459 Hypothesis 4 (a relationship between contemporary FMs and paleoclimate mean values, with
460 slow immigration and slow exclusion) was supported for MAP in North and South America.
461 Thus, all of the scenarios of **Figure 1** received some support in either North or South America.
462 The general implication is that processes of species immigration or exclusion can sometimes be
463 slow, leading to spatial variation in colonization and extinction debts across these continents.

464 The results therefore do not map cleanly onto any one class of dynamics dominating at
465 continental scales. Elucidating the details of these sometimes slow immigration and exclusion
466 dynamics more precisely would require comparing time series of functional composition to time
467 series of paleoclimate (Blonder *et al.*, 2017). That approach contrasts with the approach taken in
468 the present study, which compared time series of paleoclimate to a single time-point estimate of
469 functional composition, and tested hypotheses most relevant for single linear climate changes.
470 Time series data for functional composition are highly challenging to obtain from available
471 paleoproxies. However, such data would enable direct measurement of the rates and lags in
472 temporal response of functional composition to climate variation.

473 Results in North America are consistent with limited dispersal after ice sheet retreat
474 (Davis & Shaw, 2001, Morueta-Holme *et al.*, 2013, Svenning *et al.*, 2015), and on thermal
475 tolerances that constrain species distributions in high-latitude environments (Hawkins *et al.*,
476 2013, Körner, 2003, Morin & Lechowicz, 2011, Sakai & Weiser, 1973). The paleoclimate
477 MAT signal seen in these data may be driven by cooling in temperate and boreal portions of the
478 continent during the last glacial period that have caused regional extinctions and slow
479 recolonization dynamics (Davis, 1984). These findings extend the spatial and temporal extent of
480 analyses exploring glacial effects on biodiversity (Ordonez & Svenning, 2017), providing
481 additional confidence that this period plays a key role in shaping contemporary biodiversity
482 patterns.

483 Results in South America supported the role for paleoprecipitation variation in shaping
484 contemporary biodiversity patterns in tropical areas (Blach-Overgaard *et al.*, 2013, Gödel *et al.*,
485 2015, Rakotoarinivo *et al.*, 2013), possibly by survival and recolonization from refugia along
486 hydrological gradients. Lower precipitation values and higher precipitation temporal variation in
487 the Late Pleistocene in certain coastal regions of this continent have led to contemporary FD
488 being lower than expected based on contemporary climate. The strong precipitation effects in
489 South America caused by Northern hemisphere ice melting during the 17 ka Heinrich event and
490 the Younger Dryas are consistent with strong cross-hemisphere telecoupling of climate during
491 these intervals, in which ice sheets and ice melting in the Northern hemisphere caused
492 atmospheric and ocean circulation changes, leading to changes in Southern hemisphere climate
493 regimes (Clement & Peterson, 2008, Jones *et al.*, 2018). This result suggests that other climate
494 telecoupling may also drive initially unintuitive relationships between climate change and
495 functional composition change.

496 The spatial uncertainties in our results are possibly large. Biases in trait data coverage
497 could spatially bias our maps of FMs and FD if botanical collecting effort in certain areas were
498 focused on certain taxonomic or functional groups (Borgy *et al.*, 2017b). Because our maps of
499 functional composition are broadly consistent with other estimates (Butler *et al.*, 2017, Simova *et*
500 *al.*, 2018, van Bodegom *et al.*, 2014), this is unlikely to be a major concern. Nevertheless, trait
501 data and species occurrence are poor in some regions (e.g. the central Amazon, as well as
502 southern South America). Thus, this approach is unlikely to be able to parse out sub-regional
503 biodiversity patterns because of limitations in available data. The spatial resolution of
504 paleoclimate simulations ($>2^\circ$ per grid cell) also limits parsing of sub-regional spatial patterns
505 due to within-pixel climate heterogeneity (Stein *et al.*, 2014). Nevertheless, the broad
506 consistency of our findings across methodological choices gives some confidence in the
507 generality of our conclusions.

508 The temporal uncertainties in our results are probably smaller than the spatial
509 uncertainties. The HadCM3 simulations included multi-millennial drivers of climate change
510 (orbit, greenhouse gases, ice sheets), as well as the Heinrich event at 17 ka (Hemming, 2004) and
511 the Younger Dryas event at 13 ka (Alley, 2000). Detailed simulations of similar events in deeper
512 time were not available (e.g. the Heinrich event at ~ 45 ka (Hemming, 2004), or Dansgaard-
513 Oeschger millennial events that may increase the variability of temperature and precipitation,
514 especially between 30 and 60 ka), but it is possible that these events also have large and
515 persistent effects on contemporary functional composition. Regardless, these models provide
516 some of the best available estimates of past climates, though independent paleo-proxy validation
517 of predictions remain sparse, especially in South America (Harrison *et al.*, 2014).

518 Non-climate factors may also be important drivers of functional composition over
519 multiple timescales. For example, past human impacts on landscapes via active propagation, land
520 clearance, or fire regimes (Bond & Keeley, 2005, Keeley *et al.*, 2011) are widely acknowledged
521 throughout tropical (Levis *et al.*, 2017, Malhi, 2018, Ross, 2011) and temperate (Abrams &
522 Nowacki, 2008, Borgy *et al.*, 2017a, Feng *et al.*, 2017, Nowacki & Abrams, 2008) regions. Soil
523 and surficial geology may also be important in determining plant species distributions (Ordoñez
524 *et al.*, 2009). However, the mechanisms linking specific traits to different non-climate abiotic
525 variables are not yet completely clear. Moreover, all of these variables remain difficult and
526 controversial to estimate over time and space. While we were unable to include them in our
527 analysis, there is likely scope to extend our approach as datasets improve.

528 Climate may also indirectly drive changes in functional composition through changes in
529 species interactions. Megafauna had large impacts on plant assemblages. These impacts would
530 have shifted after the extinction of many megafauna in North and South America during the late
531 Pleistocene (Gill *et al.*, 2009, Johnson, 2009). While humans are acknowledged to be a major
532 driver of these extinctions (Lorenzen *et al.*, 2011), many also were strongly linked to climate
533 change during this period on these continents (Bartlett *et al.*, 2016). Indeed, some of the changes
534 in immigration and exclusion rates could have been driven indirectly by these organisms, e.g.
535 reduction in seed dispersal services leading to slow immigration (Pires *et al.*, 2018) (but see (van
536 Zonneveld *et al.*, 2018)), or reduced trampling leading to slow exclusion (Bakker *et al.*, 2016).
537 The temporal and spatial dynamics of megafaunal distributions remains poorly constrained by
538 data, but such information may ultimately provide additional insight into climate-linked drivers
539 of plant functional composition.

540 Our findings suggest that when predicting the future response of biodiversity to climate
541 change, disequilibrium effects due to slow immigration or exclusion may be important.
542 Statistical models based on the assumption that trait-environment relationships calibrated from
543 contemporary climate data are at equilibrium (Laughlin *et al.*, 2012, Shipley *et al.*, 2006) could
544 potentially be improved by incorporating paleoclimate predictors. Alternatively, it could be
545 useful to include more mechanistically model processes of slow immigration and/or exclusion
546 dynamics (Blonder *et al.*, 2017, Fukami, 2015, Svenning *et al.*, 2015). Such models, e.g.
547 demography-constrained species distribution models (Zurell *et al.*, 2016) or dynamic global
548 vegetation models (van Bodegom *et al.*, 2014), can represent disequilibrium dynamics that may
549 result in nonlinear relationships between climate, paleoclimate, and functional traits.

550 The overall conclusion of our study is that functional trait patterns are predicted better by
551 inclusion of paleoclimate than by contemporary climate alone, as seen via a Pleistocene
552 temperature legacy in North America and a precipitation legacy in South America. While current
553 functional composition may be well-adapted to contemporary environments, the high importance
554 of paleoclimate suggests that the equilibrium assumption of functional ecology may be
555 inappropriate for plant functional traits over 10^3 - 10^5 yr timescales and continental spatial scales.
556 The interplay between contemporary climate and paleoclimate drivers of biodiversity patterns
557 will need to be better understood in order to accurately predict assemblage responses to future
558 climate change.

559 Acknowledgements

560 BB was supported by a UK Natural Environment Research Council independent research
561 fellowship (NE/M019160/1) and the Norwegian Research Council (KLIMAFORSK 250233).
562 JCS was supported by the European Research Council (ERC-2012-StG-310886-HISTFUNC),
563 and also considers this work a contribution to his VILLUM Investigator project (VILLUM
564 Fonden grant 16549). NMH was supported by the Carlsberg Foundation and acknowledges the
565 Danish National Research Foundation for support to the Center for Macroecology, Evolution and
566 Climate. IS was supported by the Czech Science Foundation (16-26369S). CV was supported by
567 the European Research Council (ERC) Starting Grant Project “Ecophysiological and biophysical
568 constraints on domestication in crop plants” (Grant ERC-StG-2014-639706-CONSTRAINTS).
569 The study was supported by the TRY initiative on plant traits (<http://www.try-db.org>), which is
570 hosted, developed, and maintained at the Max Planck Institute for Biogeochemistry, and further
571 supported by DIVERSITAS/Future Earth and the German Centre for Integrative Biodiversity
572 Research (iDiv) Halle-Jena-Leipzig. This work was conducted as part of the Botanical
573 Information and Ecology Network (BIEN) Working Group (PIs BJE, R. Condit, RK Peet, B
574 Boyle, S Dolins and BM Thiers) supported by the National Center for Ecological Analysis and
575 Synthesis, a center funded by the National Science Foundation (EF-0553768), the University of
576 California, Santa Barbara, and the State of California. The BIEN Working Group was also
577 supported by the iPlant collaborative and the National Science Foundation (DBI-0735191). We
578 also thank all BIEN data contributors (see <http://bien.nceas.ucsb.edu/bien/people/data-providers/>
579 for a full list). Lotte Nymark Busch Jensen assisted with preparing Figure 1.

580

581 **Statement of authorship**

582 BB conceived the project and carried out analyses. JK provided trait data. JS, PV, and AO
583 provided paleoclimate data. BJE and JCS provided species occurrence data. NMH contributed to
584 species distribution modeling. All authors contributed to writing the manuscript. Authors were
585 ordered alphabetically by last name after the first author.

586

587 **Data accessibility**

588 All georeferenced data products underlying this analysis are available in **File S1** and also will be
589 deposited in Dryad upon acceptance.

590

For Review Only

References

- 591
592
593 Abrams MD, Nowacki GJ (2008) Native Americans as active and passive promoters of mast and
594 fruit trees in the eastern USA. *The Holocene*, **18**, 1123-1137.
- 595 Alley RB (2000) The Younger Dryas cold interval as viewed from central Greenland. *Quaternary*
596 *Science Reviews*, **19**, 213-226.
- 597 Asner G, Martin R, Knapp D *et al.* (2017a) Airborne laser-guided imaging spectroscopy to map
598 forest trait diversity and guide conservation. *Science*, **355**, 385-389.
- 599 Asner GP, Martin RE, Tupayachi R, Anderson CB, Sinca F, Carranza-Jiménez L, Martinez P
600 (2014) Amazonian functional diversity from forest canopy chemical assembly.
601 *Proceedings of the National Academy of Sciences*, **111**, 5604-5609.
- 602 Asner GP, Martin RE, Tupayachi R, Llactayo W (2017b) Conservation assessment of the
603 Peruvian Andes and Amazon based on mapped forest functional diversity. *Biological*
604 *Conservation*, **210**, 80-88.
- 605 Bakker ES, Gill JL, Johnson CN, Vera FW, Sandom CJ, Asner GP, Svenning J-C (2016)
606 Combining paleo-data and modern exclosure experiments to assess the impact of
607 megafauna extinctions on woody vegetation. *Proceedings of the National Academy of*
608 *Sciences*, **113**, 847-855.
- 609 Baraloto C, Timothy Paine C, Poorter L *et al.* (2010) Decoupled leaf and stem economics in rain
610 forest trees. *Ecology Letters*, **13**, 1338-1347.
- 611 Bartlett LJ, Williams DR, Prescott GW *et al.* (2016) Robustness despite uncertainty: regional
612 climate data reveal the dominant role of humans in explaining global extinctions of Late
613 Quaternary megafauna. *Ecography*, **39**, 152-161.
- 614 Bintanja R, Van De Wal RSW, Oerlemans J (2011) Modelled atmospheric temperatures and
615 global sea levels over the past million years. *Nature*, **437**, 125-128.
- 616 Bivand R, Lewin-Koh N (2013) maptools: Tools for reading and handling spatial objects. R
617 package version 0.8-29. pp Page.
- 618 Blach-Overgaard A, Kissling WD, Dransfield J, Balslev H, Svenning J-C (2013) Multimillion -
619 year climatic effects on palm species diversity in Africa. *Ecology*, **94**, 2426-2435.
- 620 Blonder B, Moulton DE, Blois J *et al.* (2017) Predictability in community dynamics. *Ecology*
621 *Letters*, **20**, 293-306.
- 622 Blonder B, Royer DL, Johnson KR, Miller I, Enquist BJ (2014) Plant Ecological Strategies Shift
623 Across the Cretaceous–Paleogene Boundary. *PLOS Biology*, **12**, e1001949.
- 624 Bond WJ, Keeley JE (2005) Fire as a global ‘herbivore’: the ecology and evolution of flammable
625 ecosystems. *Trends in Ecology & Evolution*, **20**, 387-394.

- 626 Borgy B, Violle C, Choler P *et al.* (2017a) Plant community structure and nitrogen inputs
627 modulate the climate signal on leaf traits. *Global Ecology and Biogeography*, **26**, 1138-
628 1152.
- 629 Borgy B, Violle C, Choler P *et al.* (2017b) Sensitivity of community-level trait–environment
630 relationships to data representativeness: A test for functional biogeography. *Global*
631 *Ecology and Biogeography*, **26**, 729-739.
- 632 Borgy B, Violle C, Choler P *et al.* (2017c) Sensitivity of community - level trait–environment
633 relationships to data representativeness: A test for functional biogeography. *Global*
634 *Ecology and Biogeography*, **26**, 729-739.
- 635 Boyle B, Hopkins N, Lu Z *et al.* (2013) The taxonomic name resolution service: an online tool
636 for automated standardization of plant names. *BMC bioinformatics*, **14**, 16.
- 637 Butler EE, Datta A, Flores-Moreno H *et al.* (2017) Mapping local and global variability in plant
638 trait distributions. *Proceedings of the National Academy of Sciences*, 201708984.
- 639 Campbell ID, Mcandrews JH (1993) Forest disequilibrium caused by rapid Little Ice Age
640 cooling. *Nature*, **366**, 336-338.
- 641 Chapin FS, Zavaleta ES, Eviner VT *et al.* (2000) Consequences of changing biodiversity. *Nature*,
642 **405**, 234-242.
- 643 Clement AC, Peterson LC (2008) Mechanisms of abrupt climate change of the last glacial
644 period. *Reviews of Geophysics*, **46**, n/a-n/a.
- 645 Cole LE, Bhagwat SA, Willis KJ (2014) Recovery and resilience of tropical forests after
646 disturbance. *Nature communications*, **5**, 3906.
- 647 Cornwell WK, Ackerly DD (2009) Community assembly and shifts in plant trait distributions
648 across an environmental gradient in coastal California. *Ecological Monographs*, **79**, 109-
649 126.
- 650 Cornwell WK, Schilck DW, Ackerly DD (2006) A trait - based test for habitat filtering: convex
651 hull volume. *Ecology*, **87**, 1465-1471.
- 652 Davis MB (1984) Climatic instability, time, lags, and community disequilibrium. In: *Community*
653 *Ecology*. (eds Diamond J, Case TJ) pp Page. New York, Harper & Row.
- 654 Davis MB, Shaw RG (2001) Range Shifts and Adaptive Responses to Quaternary Climate
655 Change. *Science*, **292**, 673-679.
- 656 De Bello F, Lepš J, Sebastià MT (2006) Variations in species and functional plant diversity
657 along climatic and grazing gradients. *Ecography*, **29**, 801-810.

- 658 Devictor V, Julliard R, Couvet D, Jiguet F (2008) Birds are tracking climate warming, but not
659 fast enough. *Proceedings of the Royal Society of London B: Biological Sciences*, **275**,
660 2743-2748.
- 661 DíAz S, Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem
662 processes. *Trends in Ecology & Evolution*, **16**, 646-655.
- 663 Díaz S, Kattge J, Cornelissen JH *et al.* (2016) The global spectrum of plant form and function.
664 *Nature*, **529**, 167-171.
- 665 Ehlers J, Gibbard P, Hughes P (2011) Quaternary glaciations—extent and chronology. A closer
666 look. In: *Developments in Quaternary Science*. pp Page. Amsterdam, Elsevier.
- 667 Eiserhardt WL, Borchsenius F, Plum CM, Ordonez A, Svenning J-C (2015) Climate-driven
668 extinctions shape the phylogenetic structure of temperate tree floras. *Ecology Letters*, **18**,
669 263-272.
- 670 Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction
671 across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677-
672 697.
- 673 Engemann K, Sandel B, Boyle B *et al.* (2016) A plant growth form dataset for the New World.
674 *Ecology*, **97**, 3243-3243.
- 675 Enquist BJ, Condit R, Peet RK, Schildhauer M, Thiers B (2009) The Botanical Information and
676 Ecology Network (BIEN): Cyberinfrastructure for an integrated botanical information
677 network to investigate the ecological impacts of global climate change on plant
678 biodiversity. pp Page.
- 679 Enquist BJ, Norberg J, Bonser SP *et al.* (2015) Scaling from traits to ecosystems: developing a
680 general trait driver theory via integrating trait-based and metabolic scaling theories.
681 *Advances in Ecological Research*, **52**, 249-318.
- 682 Enquist BJ, Sandel B, Boyle B *et al.* (in preparation) Plant diversity in the Americas is driven by
683 climatic-linked differences in evolutionary rates and competitive displacement.
- 684 Feng G, Mao L, Benito BM, Swenson NG, Svenning J-C (2017) Historical anthropogenic
685 footprints in the distribution of threatened plants in China. *Biological Conservation*, **210**,
686 3-8.
- 687 Fukami T (2015) Historical Contingency in Community Assembly: Integrating Niches, Species
688 Pools, and Priority Effects. *Annual Review of Ecology, Evolution, and Systematics*, **46**,
689 1-23.
- 690 Fukami T, Martijn Bezemer T, Mortimer SR, Putten WH (2005) Species divergence and trait
691 convergence in experimental plant community assembly. *Ecology Letters*, **8**, 1283-1290.

- 692 Geladi P, Kowalski BR (1986) Partial least-squares regression: a tutorial. *Analytica chimica acta*,
693 **185**, 1-17.
- 694 Gill JL, Williams JW, Jackson ST, Lininger KB, Robinson GS (2009) Pleistocene megafaunal
695 collapse, novel plant communities, and enhanced fire regimes in North America. *Science*,
696 **326**, 1100-1103.
- 697 Göldel B, Kissling WD, Svenning J-C (2015) Geographical variation and environmental
698 correlates of functional trait distributions in palms (*Arecaceae*) across the New World.
699 *Botanical Journal of the Linnean Society*, **179**, 602-617.
- 700 Grime JP (1974) Vegetation classification by reference to strategies. *Nature*, **250**, 26-31.
- 701 Habel K, Grasman R, Gramacy RB, Stahel A, Sterratt DC (2015) geometry: Mesh Generation
702 and Surface Tessellation. R package version 0.3-6. . pp Page.
- 703 Harrison SP, Bartlein PJ, Brewer S *et al.* (2014) Climate model benchmarking with glacial and
704 mid-Holocene climates. *Climate Dynamics*, **43**, 671-688.
- 705 Hawkins BA, Rueda M, Rangel TF, Field R, Diniz-Filho JaF (2013) Community phylogenetics
706 at the biogeographical scale: cold tolerance, niche conservatism and the structure of
707 North American forests. *Journal of Biogeography*, **41**, 23-28.
- 708 Hemming SR (2004) Heinrich events: Massive late Pleistocene detritus layers of the North
709 Atlantic and their global climate imprint. *Reviews of Geophysics*, **42**, n/a-n/a.
- 710 Hijmans RJ, Van Etten J (2014) raster: Geographic data analysis and modeling. R package
711 version, **2**.
- 712 Hoogakker BaA, Smith RS, Singarayer JS *et al.* (2016) Terrestrial biosphere changes over the
713 last 120 kyr. *Climate of the Past*, **12**, 51-73.
- 714 Hooper DU, Chapin F, Ewel J *et al.* (2005) Effects of biodiversity on ecosystem functioning: a
715 consensus of current knowledge. *Ecological Monographs*, **75**, 3-35.
- 716 Jetz W, Cavender-Bares J, Pavlick R *et al.* (2016) Monitoring plant functional diversity from
717 space. *Nature Plants*, **2**, 16024.
- 718 Johnson CN (2009) Ecological consequences of Late Quaternary extinctions of megafauna.
719 *Proceedings of the Royal Society of London B: Biological Sciences*, rspb. 2008.1921.
- 720 Jones TR, Roberts WHG, Steig EJ, Cuffey KM, Markle BR, White JWC (2018) Southern
721 Hemisphere climate variability forced by Northern Hemisphere ice-sheet topography.
722 *Nature*, **554**, 351.
- 723 Karger DN, Conrad O, Böhner J *et al.* (2016) CHELSA climatologies at high resolution for the
724 earth's land surface areas (Version 1.1).

- 725 Kattge J, Díaz S, Lavorel S *et al.* (2011) TRY – a global database of plant traits. *Global Change*
726 *Biology*, **17**, 2905-2935.
- 727 Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA (2011) Fire as an evolutionary
728 pressure shaping plant traits. *Trends Plant Sci*, **16**, 406-411.
- 729 Kleman J, Fastook J, Ebert K, Nilsson J, Caballero R (2013) Pre-LGM Northern Hemisphere ice
730 sheet topography. *Climate of the Past*, **9**, 2365.
- 731 Kleman J, Jansson K, De Angelis H, Stroeven AP, Hättstrand C, Alm G, Glasser N (2010)
732 North American Ice Sheet build-up during the last glacial cycle, 115–21kyr. *Quaternary*
733 *Science Reviews*, **29**, 2036-2051.
- 734 Körner C (2003) *Alpine plant life: functional plant ecology of high mountain ecosystems; with 47*
735 *tables*, Springer Science & Business Media.
- 736 Krämer N, Sugiyama M (2011) The Degrees of Freedom of Partial Least Squares Regression.
737 *Journal of the American Statistical Association*, **106**, 697-705.
- 738 La Sorte FA, Jetz W (2012) Tracking of climatic niche boundaries under recent climate change.
739 *Journal of Animal Ecology*, **81**, 914-925.
- 740 Lamanna C, Blonder B, Violle C *et al.* (2014) Functional trait space and the latitudinal diversity
741 gradient. *Proceedings of the National Academy of Sciences*, **111**, 13745-13750.
- 742 Laughlin DC, Joshi C, Bodegom PM, Bastow ZA, Fulé PZ (2012) A predictive model of
743 community assembly that incorporates intraspecific trait variation. *Ecology Letters*, **15**,
744 1291-1299.
- 745 Levis C, Costa FR, Bongers F *et al.* (2017) Persistent effects of pre-Columbian plant
746 domestication on Amazonian forest composition. *Science*, **355**, 925-931.
- 747 Li B, Morris J, Martin EB (2002) Model selection for partial least squares regression.
748 *Chemometrics and Intelligent Laboratory Systems*, **64**, 79-89.
- 749 Lorenzen ED, Nogués-Bravo D, Orlando L *et al.* (2011) Species-specific responses of Late
750 Quaternary megafauna to climate and humans. *Nature*, **479**, 359.
- 751 Maitner BS, Boyle B, Casler N *et al.* (2017) The bien r package: A tool to access the Botanical
752 Information and Ecology Network (BIEN) database. *Methods in Ecology and Evolution*,
753 **9**, 373-379.
- 754 Malhi Y (2018) Ancient deforestation in the green heart of Africa. *Proceedings of the National*
755 *Academy of Sciences*, 201802172.
- 756 Mathieu J, Jonathan Davies T (2014) Glaciation as an historical filter of below-ground
757 biodiversity. *Journal of Biogeography*, **41**, 1204-1214.

- 758 Mevik B-H, Wehrens R (2007) The pls Package: Principal Component and Partial Least Squares
759 Regression in R. *Journal of Statistical Software*; Vol 1, Issue 2 (2007).
- 760 Moles AT, Perkins SE, Laffan SW *et al.* (2014) Which is a better predictor of plant traits:
761 temperature or precipitation? *Journal of Vegetation Science*, **25**, 1167-1180.
- 762 Morin X, Lechowicz MJ (2011) Geographical and ecological patterns of range size in North
763 American trees. *Ecography*, **34**, 738-750.
- 764 Morley R (2011) Cretaceous and Tertiary climate change and the past distribution of
765 megathermal rainforests. In: *Tropical rainforest responses to climatic change*. pp Page.,
766 Springer.
- 767 Morueta-Holme N, Enquist BJ, McGill BJ *et al.* (2013) Habitat area and climate stability
768 determine geographical variation in plant species range sizes. *Ecology Letters*, **16**, 1446-
769 1454.
- 770 Nowacki GJ, Abrams MD (2008) The demise of fire and “mesophication” of forests in the
771 eastern United States. *BioScience*, **58**, 123-138.
- 772 Ordonez A, Svenning J-C (2015) Geographic patterns in functional diversity deficits are linked
773 to glacial-interglacial climate stability and accessibility. *Global Ecology and*
774 *Biogeography*, **24**, 826-837.
- 775 Ordonez A, Svenning J-C (2016) Functional diversity of North American broad-leaved trees is
776 codetermined by past and current environmental factors. *Ecosphere*, **7**, e01237-n/a.
- 777 Ordonez A, Svenning J-C (2017) Consistent role of Quaternary climate change in shaping
778 current plant functional diversity patterns across European plant orders. *Scientific*
779 *Reports*, **7**, 42988.
- 780 Ordoñez JC, Van Bodegom PM, Witte JPM, Wright IJ, Reich PB, Aerts R (2009) A global study
781 of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global*
782 *Ecology and Biogeography*, **18**, 137-149.
- 783 Pires MM, Guimarães PR, Galetti M, Jordano P (2018) Pleistocene megafaunal extinctions and
784 the functional loss of long - distance seed - dispersal services. *Ecography*, **41**, 153-163.
- 785 Polly PD, Eronen JT, Fred M *et al.* (2011) History matters: eometrics and integrative climate
786 change biology. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1131-
787 1140.
- 788 Rakotoarinivo M, Blach-Overgaard A, Baker WJ, Dransfield J, Moat J, Svenning J-C (2013)
789 Palaeo-precipitation is a major determinant of palm species richness patterns across
790 Madagascar: a tropical biodiversity hotspot. *Proceedings of the Royal Society of London*
791 *B: Biological Sciences*, **280**, 20123048.

- 792 Raunkiær CC (1907) *Planterigets livsformer og deres betydning for geografin*, København og
793 Kristiania, Gyldendalske boghandel, Nordisk forlag.
- 794 Ross NJ (2011) Modern tree species composition reflects ancient Maya “forest gardens” in
795 northwest Belize. *Ecological Applications*, **21**, 75-84.
- 796 Sakai A, Weiser C (1973) Freezing resistance of trees in North America with reference to tree
797 regions. *Ecology*, **54**, 118-126.
- 798 Schimper AFW (1898) *Pflanzen-geographie auf physiologischer Grundlage*, Jena, Gustav
799 Fischer.
- 800 Schrodte F, Kattge J, Shan H *et al.* (2015) BHPMF-a hierarchical Bayesian approach to gap -
801 filling and trait prediction for macroecology and functional biogeography. *Global*
802 *Ecology and Biogeography*, **24**, 1510-1521.
- 803 Shipley B, Vile D, Garnier É (2006) From plant traits to plant communities: a statistical
804 mechanistic approach to biodiversity. *Science*, **314**, 812-814.
- 805 Simova I, Engemann K, Wiser S *et al.* (2018) Spatial patterns and climate relationships of major
806 plant traits in the New World differ between woody and non-woody species. *Journal of*
807 *Biogeography*, **in press**.
- 808 Šímová I, Violle C, Kraft NJ *et al.* (2015) Shifts in trait means and variances in North American
809 tree assemblages: species richness patterns are loosely related to the functional space.
810 *Ecography*, **38**, 649-658.
- 811 Singarayer JS, Valdes PJ (2010) High-latitude climate sensitivity to ice-sheet forcing over the
812 last 120 kyr. *Quaternary Science Reviews*, **29**, 43-55.
- 813 Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species
814 richness across taxa, biomes and spatial scales. *Ecology Letters*, **17**, 866-880.
- 815 Svenning J-C, Eiserhardt WL, Normand S, Ordoñez A, Sandel B (2015) The Influence of
816 Paleoclimate on Present-Day Patterns in Biodiversity and Ecosystems. *Annual Review of*
817 *Ecology, Evolution, and Systematics*, **46**, 551-572.
- 818 Svenning J-C, Sandel B (2013) Disequilibrium vegetation dynamics under future climate change.
819 *American Journal of Botany*, **100**, 1266-1286.
- 820 Svenning J-C, Skov F (2007) Could the tree diversity pattern in Europe be generated by
821 postglacial dispersal limitation? *Ecology Letters*, **10**, 453-460.
- 822 Swenson NG, Enquist BJ, Pither J *et al.* (2012) The biogeography and filtering of woody plant
823 functional diversity in North and South America. *Global Ecology and Biogeography*, **21**,
824 798-808.

- 825 Thuiller W, Albert C, Araújo MB *et al.* (2008) Predicting global change impacts on plant
826 species' distributions: future challenges. *Perspectives in plant ecology, evolution and*
827 *systematics*, **9**, 137-152.
- 828 Van Bodegom PM, Douma JC, Verheijen LM (2014) A fully traits-based approach to modeling
829 global vegetation distribution. *Proceedings of the National Academy of Sciences*, **111**,
830 13733-13738.
- 831 Van Zonneveld M, Larranaga N, Blonder B, Coradin L, Hormaza JI, Hunter D (2018) Human
832 diets drive range expansion of megafauna-dispersed fruit species. *Proceedings of the*
833 *National Academy of Sciences*, **115**, 3326-3331.
- 834 Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices
835 for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290-2301.
- 836 Violle C, Reich PB, Pacala SW, Enquist BJ, Kattge J (2014) The emergence and promise of
837 functional biogeography. *Proceedings of the National Academy of Sciences*, **111**, 13690-
838 13696.
- 839 Von Humboldt A, Bonpland A (eds) (1807 (tr. 2009)) *Essay on the Geography of Plants*, Paris,
840 University of Chicago Press.
- 841 Webb T (1986) Is vegetation in equilibrium with climate? How to interpret late-Quaternary
842 pollen data. *Vegetatio*, **67**, 75-91.
- 843 Westoby M, Wright IJ (2006) Land-plant ecology on the basis of functional traits. *Trends in*
844 *Ecology & Evolution*, **21**, 261-268.
- 845 Woodruff DS (2010) Biogeography and conservation in Southeast Asia: how 2.7 million years of
846 repeated environmental fluctuations affect today's patterns and the future of the
847 remaining refugial-phase biodiversity. *Biodiversity and Conservation*, **19**, 919-941.
- 848 Zurell D, Thuiller W, Pagel J *et al.* (2016) Benchmarking novel approaches for modelling
849 species range dynamics. *Global Change Biology*, **22**, 2651–2664.
850
- 851

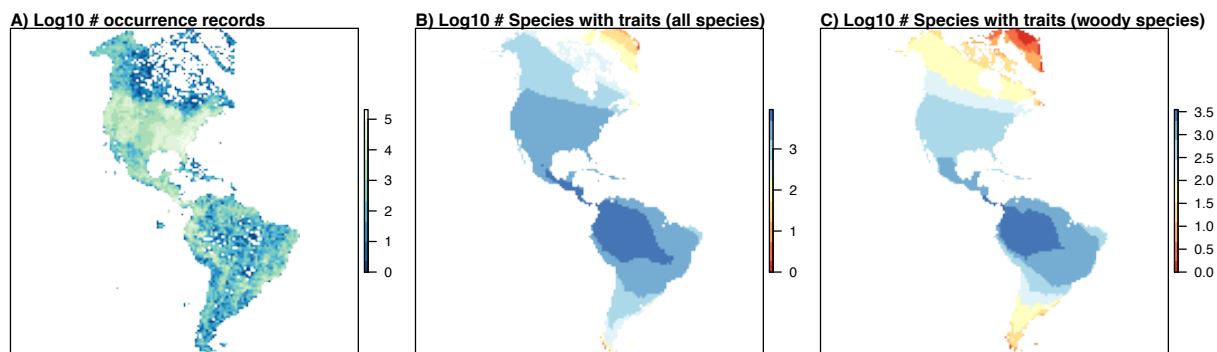
852 **Supporting Information**

853

854 **File S1** – Processed raster maps (ASCII grid format) for FMs, FD, FD_{res}, and contemporary and
855 paleoclimate means and temporal standard deviations. Includes metadata file (PDF format)
856 explaining data variables, units, and provenance.

For Review Only

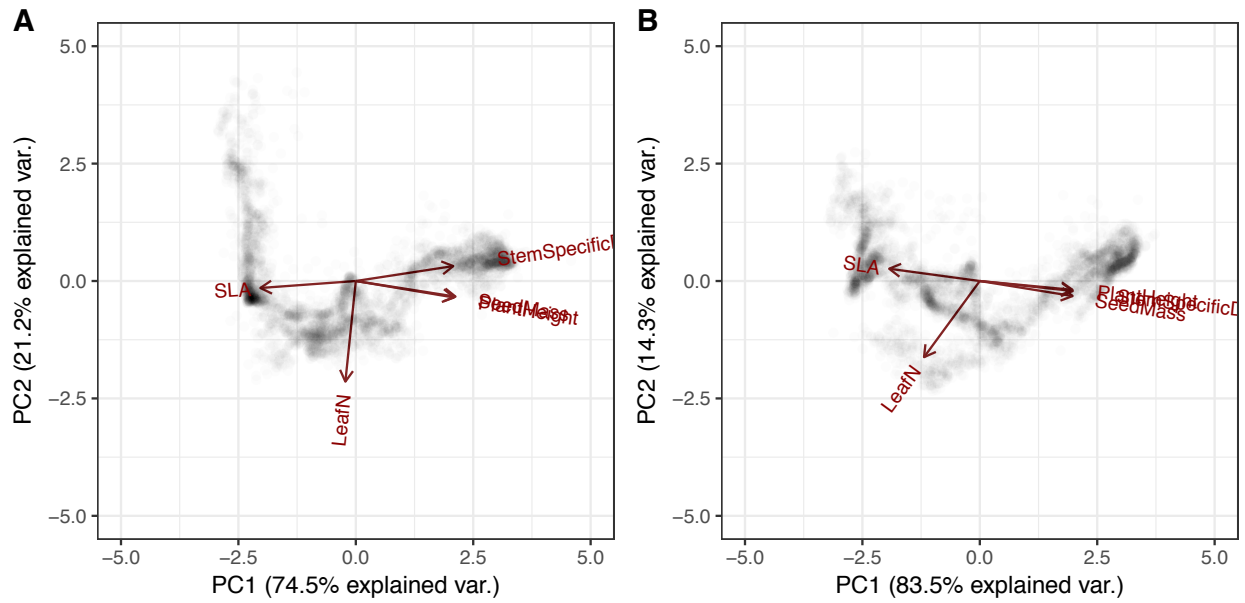
857 **Figure S1.** Summary of data coverage. A) Raw counts of occurrences for the BIEN3 database.
858 B) Number of species for which trait data were available. C) Number of woody species for
859 which trait data were available. Note \log_{10} scale for all panels.



860

For Review Only

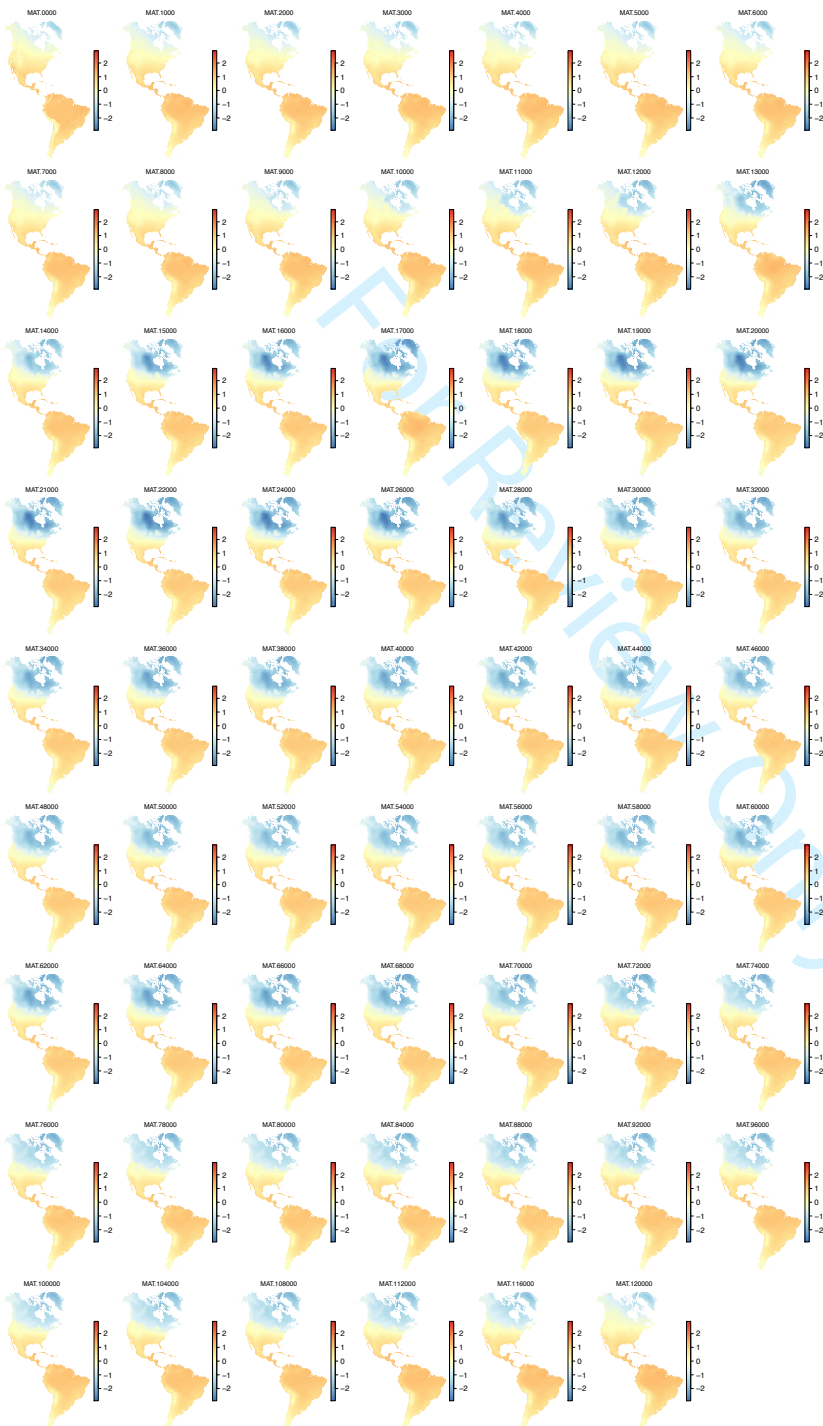
861 **Figure S2.** Principal component analysis of log-transformed trait values for **A)** all species and **B)**
862 only woody species.



863

Review Only

864 **Figure S3.** Paleotemperature predictions from the HadCM3 model for 0 – 120 ka. Values are
865 reported in scaled coordinates relative to mean and standard deviation across all pixels and all
866 times.



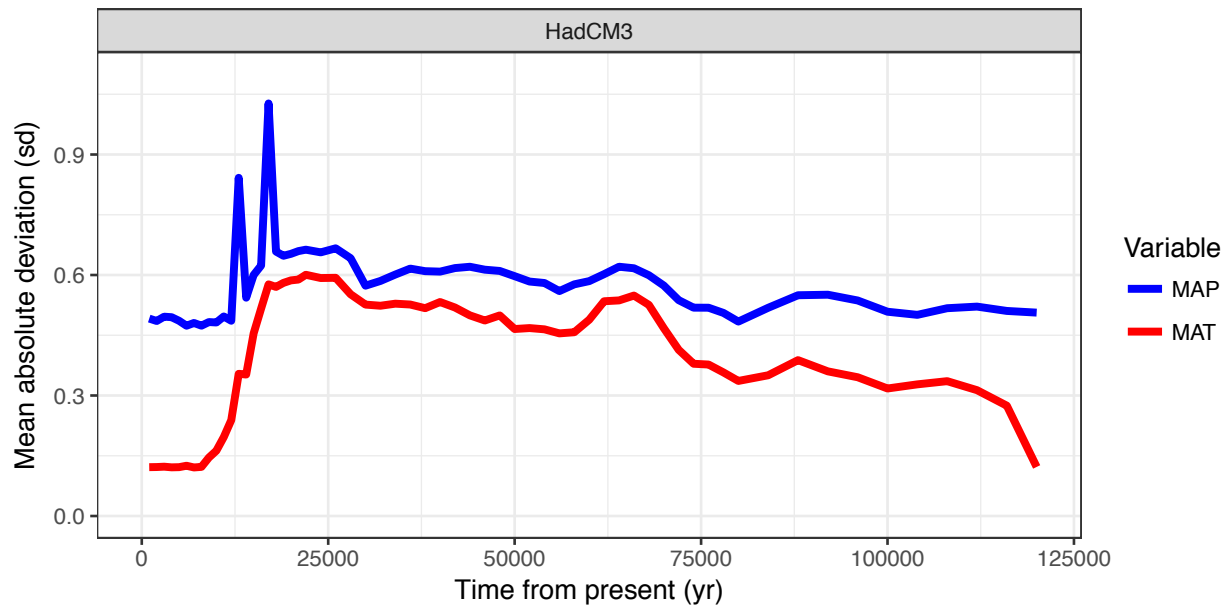
867

868 **Figure S4.** Paleoprecipitation predictions from the HadCM3 model for 0 – 120 ka. Values are
869 reported in scaled coordinates relative to mean and standard deviation across all pixels and all
870 times.



871

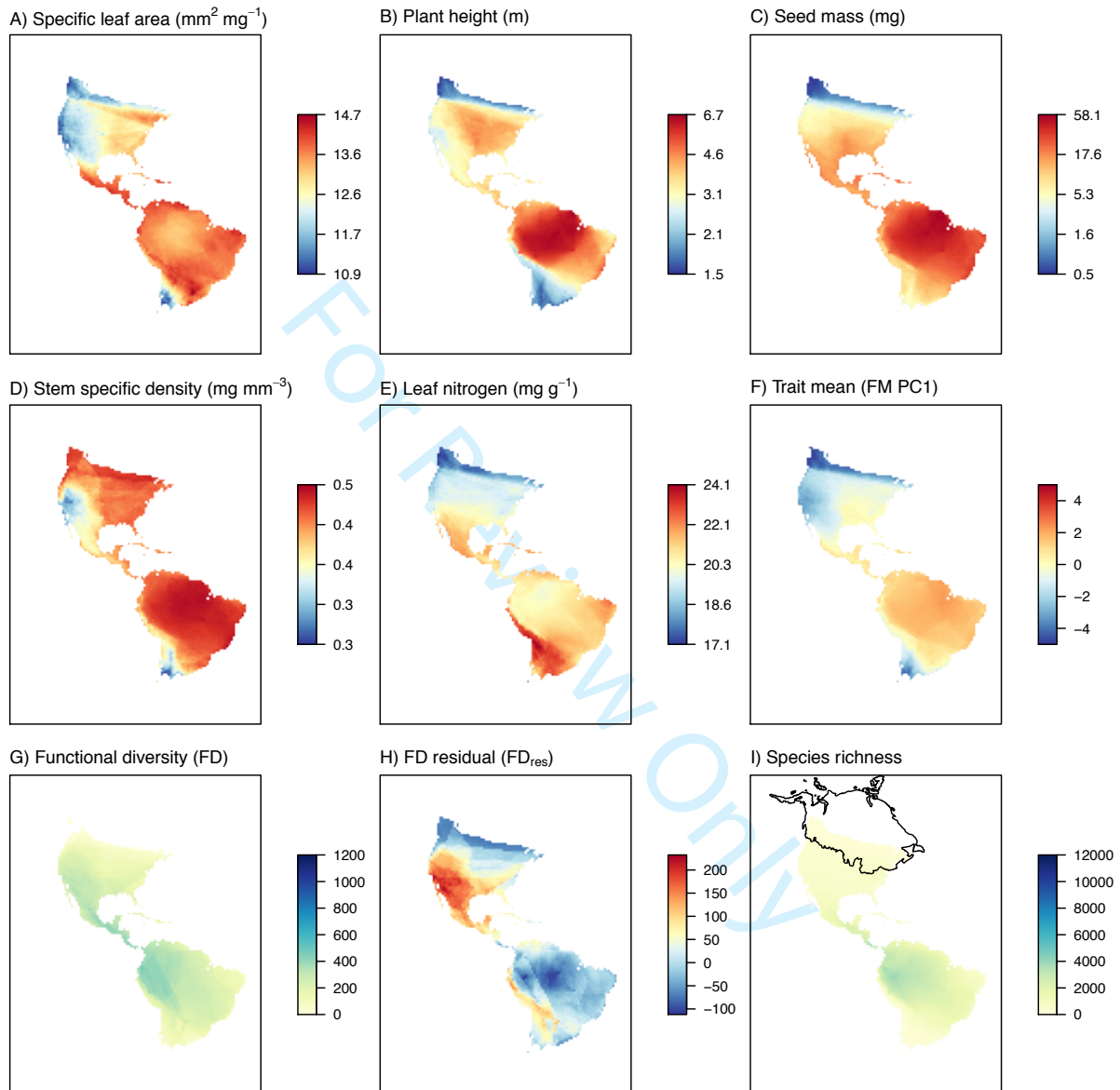
872 **Figure S5.** Deviation between present-day climate and paleoclimates at different past times for
873 the HadCM3 model. Y-axis values indicate the mean absolute deviation between contemporary
874 and paleoclimate pixel values in transformed coordinates (standard deviations relative to 0-120
875 ka ranges). Blue lines, mean annual precipitation; red lines, mean annual temperature.



876

877

878 **Figure S6.** Estimated plant species assemblage characteristics, based on data for only woody
879 species. Compare caption to **Figure 3**.

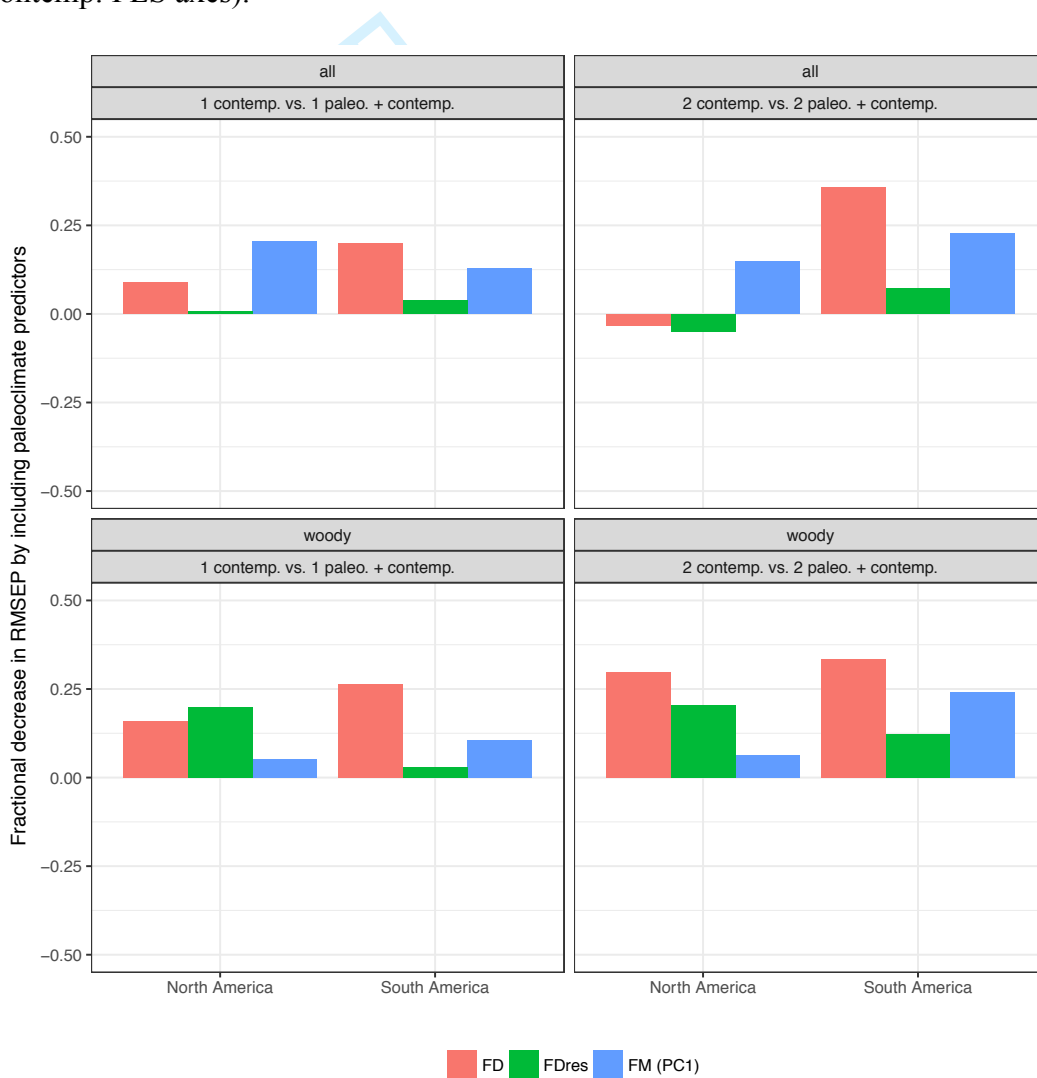


880

881

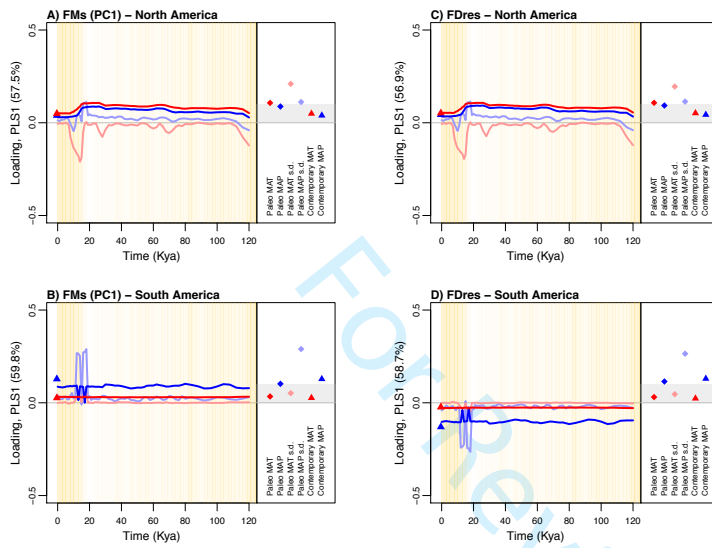
882

883 **Figure S7.** Predictive ability of PLS models usually increases when including paleoclimate
 884 predictors as well as contemporary climate predictors. Bar height indicates percent decrease in
 885 RMSEP of each model (paleo. + contemp. relative to contemp. only) for different variables (bar
 886 colors – red, FD, green FD_{res} , blue, FM (PC1)). Plots are shown for models for each continent,
 887 and for every combination of trait data (woody vs. all species) and number of PLS components
 888 (1 contemp. PLS axis vs. 1 paleo. + contemp. PLS axis, or 2 contemp. PLS axes vs 2 paleo. +
 889 contemp. PLS axes).



890

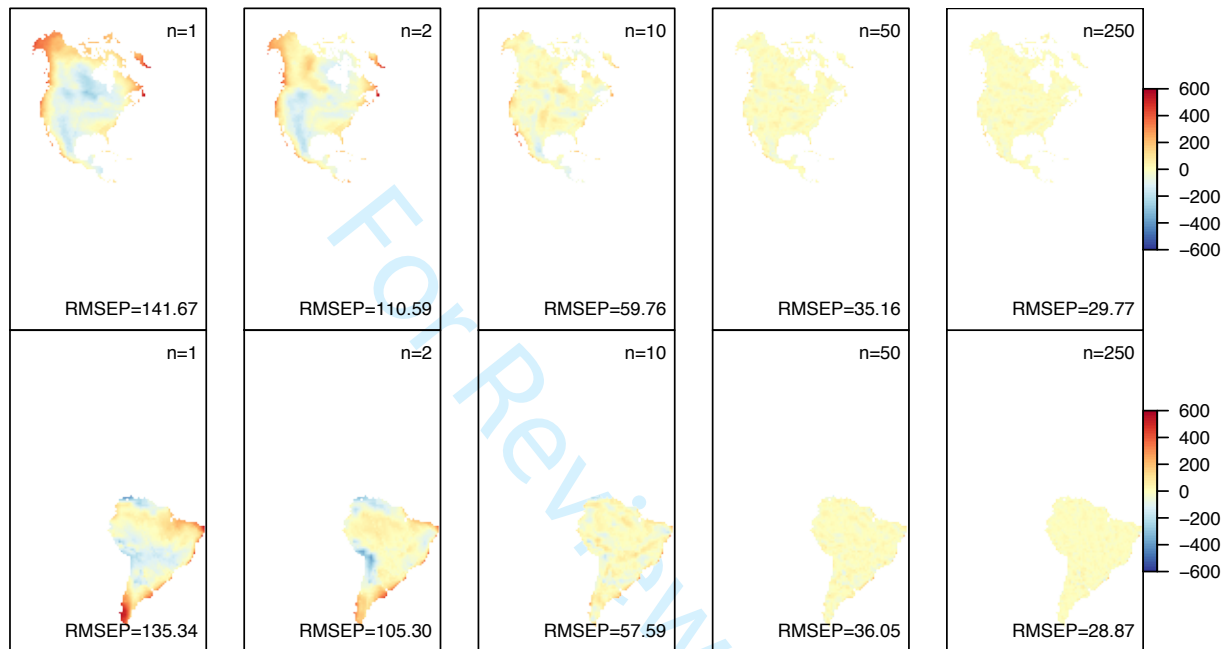
891 **Figure S8.** Contemporary climate and paleoclimate effects on contemporary FMs (PC1) (A,B)
892 and FD_{res} (C,D) using trait data for all species and climate data from HadCM3. Compare caption
893 to **Figure 5.**



894

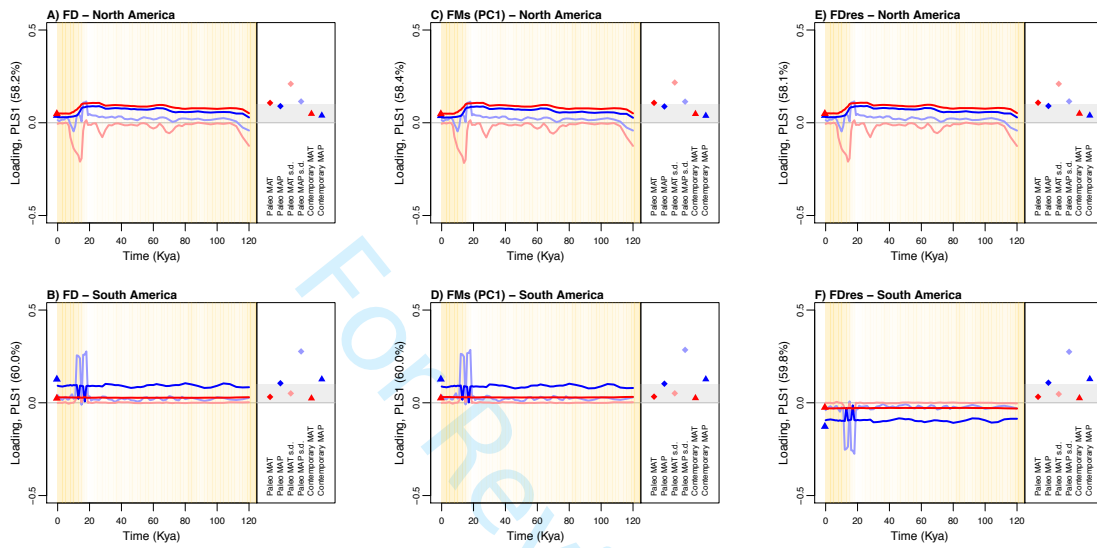
895

896 **Figure S9.** Residuals of PLS regression model for FD. Results are based on trait data for all
897 species and climate data from HadCM3. Panels indicate the number of PLS components included
898 in the model (n) and the cross-validated root mean square error of prediction (RMSEP). Over-
899 predicted values are shown in red and under-predicted values are shown in blue.



900

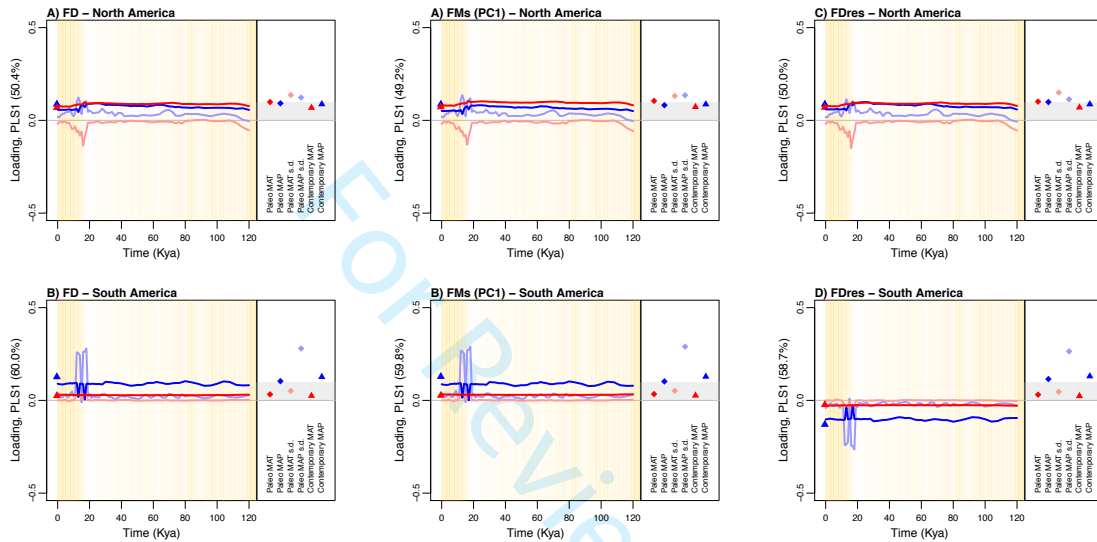
901 **Figure S10.** Contemporary climate and paleoclimate effects on contemporary FD (**A,B**), FMs
 902 (PC1) (**C,D**) and FD_{res} (**E,F**) using trait data for woody species and climate data from HadCM3.
 903 Compare caption to **Figure 5**.



904

905

906 **Figure S11.** Contemporary climate and paleoclimate effects on contemporary FD (**A,B**), FMs
 907 (PC1) (**C,D**) and FD_{res} (**E,F**) using trait data for all species and climate data from HadCM3. In
 908 this analysis, locations under ice at the Last Glacial Maximum are wholly excluded from the
 909 analysis. Compare caption to **Figure 5**.



910

911

912 **Table S1.** Original data sources for trait data extracted from the TRY database.

913

914 Ackerly, D. D. and W. K. Cornwell. 2007. A trait-based approach to community assembly:
915 partitioning of species trait values into within- and among-community components. *Ecology*
916 *Letters* 10:135-145.

917 Adler, P.B. 2003. A comparison of livestock grazing effects on sagebrush steppe, USA, and
918 Patagonian steppe, Argentina. PhD Thesis, Colorado State University.

919 Adler, P.B., Milchunas, D.G., Lauenroth, W.K., Sala, O.E. & Burke, I.C. (2004) Functional traits
920 of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology*,
921 41, 653-663.

922 Adriaenssens S. 2012. Dry deposition and canopy exchange for temperate tree species under
923 high nitrogen deposition. PhD thesis, Ghent University, Ghent, Belgium, 209p.

924 Atkin, O. K., M. H. M. Westbeek, M. L. Cambridge, H. Lambers, and T. L. Pons. 1997. Leaf
925 respiration in light and darkness - A comparison of slow- and fast-growing *Poa* species. *Plant*
926 *Physiology* 113:961-965.

927 Atkin, O. K., M. Schortemeyer, N. McFarlane, and J. R. Evans. 1999. The response of fast- and
928 slow-growing *Acacia* species to elevated atmospheric CO₂: an analysis of the underlying
929 components of relative growth rate. *Oecologia* 120:544-554.

930 Auger, S. 201. MSc thesis, Université de Sherbrooke, Sherbrooke (Quebec) L'importance de la
931 variabilité interspécifique des traits fonctionnels par rapport à la variabilité intraspécifique
932 chez les jeunes arbres en forêt mature.

- 933 Auger, S., Shipley, B. 2013. Interspecific and intraspecific trait variation along short
934 environmental gradients in an old-growth temperate forest. *Journal of Vegetation Science* 24:
935 419-428.
- 936 B. Sandel, J. D. Corbin, and M. Krupa 2011. Using plant functional traits to guide restoration: A
937 case study in California coastal grassland. *Ecosphere* 2:1-16.
- 938 Bahn, M., G. Wohlfahrt, E. Haubner, I. Horak, W. Michaeler, K. Rottmar, U. Tappeiner, and A.
939 Cernusca. 1999. Leaf photosynthesis, nitrogen contents and specific leaf area of 30 grassland
940 species in differently managed mountain ecosystems in the Eastern Alps. In: Cernusca A., U.
941 Tappeiner & N. Bayfield (eds.) *Land-use changes in European mountain ecosystems.*
942 *ECOMONT- Concept and Results.* Blackwell Wissenschaft, Berlin, p. 247-255.
- 943 Baker, T. R., O.L. Phillips, W.F. Laurance, N.C.A. Pitman, S. Almeida, L. Arroyo, A. DiFiore,
944 T. Erwin, N. Higuchi, T.J. Killeen, S.G. Laurance, H. Nascimento, A. Monteagudo, D.A.
945 Neill, J.N.M. Silva, Y. Malhi, G. Lopez Gonzalez, J. Peacock, C.A. Quesada, S.L. Lewis, J.
946 Lloyd. Do species traits determine patterns of wood production in Amazonian forests?
947 *Biogeosciences* 6:297-309.
- 948 Bakker, C., J. Rodenburg, and P. Bodegom. 2005. Effects of Ca- and Fe-rich seepage on P
949 availability and plant performance in calcareous dune soils. *Plant and Soil* 275: 111-122.
- 950 Bakker, C., P. M. Van Bodegom, H. J. M. Nelissen, W. H. O. Ernst, and R. Aerts. 2006. Plant
951 responses to rising water tables and nutrient management in calcareous dune slacks. *Plant*
952 *Ecology* 185:19-28.
- 953 Baraloto, C., C. E. T. Paine, L. Poorter, J. Beauchene, D. Bonal, A.-M. Domenach, B. Herault, S.
954 Patino, J.-C. Roggy, and J. Chave. 2010. Decoupled leaf and stem economics in rainforest
955 trees. *Ecology Letters* 13:1338-1347

- 956 Baraloto, C., C. E. T. Paine, S. Patino, D. Bonal, B. Herault, and J. Chave. 2010. Functional trait
957 variation and sampling strategies in species-rich plant communities. *Functional Ecology* 24:
958 208-216
- 959 Blanco, C. C., E. E. Sosinski, B. R. C. dos Santos, M. A. da Silva, and V. D. Pillar. 2007. On the
960 overlap between effect and response plant functional types linked to grazing. *Community
961 Ecology* 8: 57-65.
- 962 Blonder, B., Buzzard, B., Sloat, L., Simova, I., Lipson, R., Boyle, B., Enquist, B. 2012. The leaf-
963 area shrinkage effect can bias paleoclimate and ecology research. *American Journal of
964 Botany* 99: 1753-1763.
- 965 Blonder, B., Vasseur, F., Violle, C., Shipley, B., Enquist, B., Vile, D. 2015. Testing models for
966 the leaf economics spectrum with leaf and whole-plant traits in *Arabidopsis thaliana* *AoB
967 Plants* 7: plv049.
- 968 Blonder, B., Violle, C., Enquist, B. 2013. Assessing the causes and scales of the leaf economics
969 spectrum using venation networks in *Populus tremuloides*. *Journal of Ecology* 101: 981-989.
- 970 Blonder, B., Violle, C., Patrick, L., Enquist, B. 2011. Leaf venation networks and the origin of
971 the leaf economics spectrum. *Ecology Letters* 14: 91-100.
- 972 Bocanegra-Gonzalez KT, Fernandez-Mendez F, Galvis-Jimenez, JF. 2017. Determinación de la
973 resiliencia en bosques secundarios húmedos tropicales a través de la diversidad funcional de
974 árboles en la región del Bajo Calima, Buenaventura, Colombia.
- 975 Bond-Lamberty, B., C. Wang, and S. T. Gower. 2002. Above- and belowground biomass and
976 sapwood area allometric equations for six boreal tree species of northern Manitoba. *Canadian
977 Journal of Forestry Research* 32: 1441-1450.

- 978 Bond-Lamberty, B., C. Wang, and S. T. Gower. 2002. Leaf area dynamics of a boreal black
979 spruce fire chronosequence, *Tree Physiology* 22: 993-1001.
- 980 Bond-Lamberty, B., C. Wang, and S. T. Gower. 2003. The use of multiple measurement
981 techniques to refine estimates of conifer needle geometry. *Canadian Journal of Forestry*
982 *Research* 33: 101-105.
- 983 Bragazza L. 2009. Conservation priority of Italian alpine habitats: a floristic approach based on
984 potential distribution of vascular plant species. *Biodiversity and Conservation* 18: 2823–
985 2835.
- 986 Brown, K.A., Flynn, D.F.B., Abram, N.K., Ingram, J.C., Johnson, S.E. & Wright, P. 2011.
987 Assessing Natural Resource Use by Forest-Reliant Communities in Madagascar Using
988 Functional Diversity and Functional Redundancy Metrics. *PLoS One*, 6: e24107.
- 989 Burrascano, S., Copiz, R., Del Vico, E., Fagiani, S., Giarrizzo, E., Mei, M., Mortelliti, A.,
990 Sabatini, F.M. & Blasi, C. 2015. Wild boar rooting intensity determines shifts in understorey
991 composition and functional traits. *Community Ecology*, 16: 244-253.
- 992 Butterfield, B.J. and J.M. Briggs. 2011. Regeneration niche differentiates functional strategies of
993 desert woody plant species. *Oecologia*, 165: 477-487.
- 994 Campbell, C., L. Atkinson, J. Zaragoza-Castells, M. Lundmark, O. Atkin, and V. Hurry. 2007.
995 Acclimation of photosynthesis and respiration is asynchronous in response to changes in
996 temperature regardless of plant functional group. *New Phytologist* 176: 375-383
- 997 Campetella, G; Botta-Dukát, Z; Wellstein, C; Canullo, R; Gatto, S; Chelli, S; Mucina, L; Bartha,
998 S. 2011. Patterns of plant trait-environment relationships along a forest succession
999 chronosequence. *Agriculture, Ecosystems & Environment* 145: 38-48

- 1000 Carswell, F. E., Meir, P., Wandelli, E. V., Bonates, L. C. M., Kruijt, B., Barbosa, E. M., Nobre,
1001 A. D. & Jarvis, P. G. 2000. Photosynthetic capacity in a central Amazonian rain forest. *Tree*
1002 *Physiology* 20: 179-186.
- 1003 Castro-Diez, P., J. P. Puyravaud, J. H. C. Cornelissen, and P. Villar-Salvador. 1998. Stem
1004 anatomy and relative growth rate in seedlings of a wide range of woody plant species and
1005 types. *Oecologia* 116:57-66.
- 1006 Cavender-Bares, J., A. Keen, and B. Miles. 2006. Phylogenetic structure of floridian plant
1007 communities depends on taxonomic and spatial scale. *Ecology* 87:S109-S122.
- 1008 Cerabolini B.E.L., Brusa G., Ceriani R.M., De Andreis R., Luzzaro A. & Pierce S. 2010. Can
1009 CSR classification be generally applied outside Britain? *Plant Ecology* 210: 253-261
- 1010 Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a
1011 world wide wood economics spectrum. *Ecology Letters* 12: 351-366.
- 1012 Chen, Y., Han, W., Tang, L., Tang, Z. & Fang, J. 2013. Leaf nitrogen and phosphorus
1013 concentrations of woody plants differ in responses to climate, soil and plant growth form.
1014 *Ecography* 36: 178-184.
- 1015 Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild,
1016 T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martinez-Vilalta,
1017 J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry,
1018 J.S., Westoby, M., Wright, I.J. & Zanne, A.E. 2012. Global convergence in the vulnerability
1019 of forests to drought. *Nature*, 491, 752-755.
- 1020 Ciocarlan V. (2009). The illustrated Flora of Romania. Pteridophyta et Spermatopyta. Editura
1021 Ceres, 1141 p (in Romanian).

- 1022 Coomes, D. A., S. Heathcote, E. R. Godfrey, J. J. Shepherd, and L. Sack. 2008. Scaling of xylem
1023 vessels and veins within the leaves of oak species. *Biology Letters* 4:302-306.
- 1024 Cornelissen, J. H. C. 1996. An experimental comparison of leaf decomposition rates in a wide
1025 range of temperate plant species and types. *Journal of Ecology* 84:573-582.
- 1026 Cornelissen, J. H. C., B. Cerabolini, P. Castro-Diez, P. Villar-Salvador, G. Montserrat-Marti, J.
1027 P. Puyravaud, M. Maestro, M. J. A. Werger, and R. Aerts. 2003. Functional traits of woody
1028 plants: correspondence of species rankings between field adults and laboratory-grown
1029 seedlings? *Journal of Vegetation Science* 14: 311-322.
- 1030 Cornelissen, J. H. C., H. M. Quested, D. Gwynn-Jones, R. S. P. Van Logtestijn, M. A. H. De
1031 Beus, A. Kondratchuk, T. V. Callaghan, and R. Aerts. 2004. Leaf digestibility and litter
1032 decomposability are related in a wide range of subarctic plant species and types. *Functional*
1033 *Ecology* 18: 779-786.
- 1034 Cornelissen, J. H. C., P. C. Diez, and R. Hunt. 1996. Seedling growth, allocation and leaf
1035 attributes in a wide range of woody plant species and types. *Journal of Ecology* 84: 755-765.
- 1036 Cornelissen, J.H.C. 1999. A triangular relationship between leaf size and seed size among woody
1037 species: allometry, ontogeny, ecology and taxonomy. *Oecologia* 118: 248-255.
- 1038 Cornwell, W. K. and D. D. Ackerly. 2009. Community assembly and shifts in plant trait
1039 distributions across an environmental gradient in coastal California. *Ecological Monographs*
1040 79: 109-126.
- 1041 Cornwell, W. K., D. W. Schwilk, and D. D. Ackerly. 2006. A trait-based test for habitat filtering:
1042 Convex hull volume. *Ecology* 87: 1465-1471.

- 1043 Cornwell, W. K., J. H. C. Cornelissen, K. Amatangelo, E. Dorrepaal, V. T. Eviner, O. Godoy, S.
1044 E. Hobbie, B. Hoorens, H. Kurokawa, N. Pérez-Harguindeguy, H. M. Queded, L. S.
1045 Santiago, D. A. Wardle, I. J. Wright, R. Aerts, S. D. Allison, P. van Bodegom, V
1046 Cornwell, W. K., R. Bhaskar, L. Sack, S. Cordell, and C. K. Lunch. 2007. Adjustment of
1047 structure and function of Hawaiian *Metrosideros polymorpha* at high vs. low precipitation.
1048 *Functional Ecology* 21: 1063-1071.
- 1049 Craine JM, Towne EG, Ocheltree TW, Nippert JB (2012) Community traitscape of foliar
1050 nitrogen isotopes reveals N availability patterns in a tallgrass prairie. *Plant Soil* 356: 395-403
- 1051 Craine, J. M., A. J. Elmore, M. P. M. Aida, M. Bustamante, T. E. Dawson, E. A. Hobbie, A.
1052 Kahmen, M. C. Mack, K. K. McLaughlan, A. Michelsen, G. B. Nardoto, L. H. Pardo, J.
1053 Penuelas, P. B. Reich, E. A. G. Schuur, W. D. Stock, P. H. Templer, R. A. Virgini
- 1054 Craine, J. M., W. G. Lee, W. J. Bond, R. J. Williams, and L. C. Johnson. 2005. Environmental
1055 constraints on a global relationship among leaf and root traits of grasses. *Ecology* 86: 12-19.
- 1056 Craven, D., D. Braden, M. S. Ashton, G. P. Berlyn, M. Wishnie, and D. Dent. 2007. Between
1057 and within-site comparisons of structural and physiological characteristics and foliar nutrient
1058 content of 14 tree species at a wet, fertile site and a dry, infertile site in Panama. *Forest
1059 Ecology and Management* 238: 335-346.
- 1060 Craven, D., D. Dent, D. Braden, M. S. Ashton, G. P. Berlyn, and J. S. Hall. 2011. Seasonal
1061 variability of photosynthetic characteristics influences growth of eight tropical tree species at
1062 two sites with contrasting precipitation in Panama. *Forest Ecology and Management* 261:
1063 1643-1653.
- 1064 Dainese M, Bragazza L. 2012. Plant traits across different habitats of the Italian Alps: a
1065 comparative analysis between native and alien species. *Alpine Botany* 122: 11-21.

- 1066 de Araujo, A.C., J. P. H. B. Ometto, A. J. Dolman, B. Kruijt, M. J. Waterloo and J. R.
1067 Ehleringer. 2011. LBA-ECO CD-02 C and N Isotopes in Leaves and Atmospheric CO₂,
1068 Amazonas, Brazil. Data set. Available on-line [<http://daac.ornl.gov>].
- 1069 Demey A, J Staelens, L Baeten, P Boeckx, M Hermy, J Kattge, K Verheyen. 2013. Nutrient
1070 input from hemiparasitic litter favors plant species with a fast-growth strategy. *Plant and Soil*
1071 371: 53-66.
- 1072 Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-
1073 Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P.,
1074 Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rantomé, M.C.,
1075 Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S.,
1076 Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A.,
1077 Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S.,
1078 Siavash, B., Villar-Salvador, P. & Zak, M.R. 2004. The plant traits that drive ecosystems:
1079 Evidence from three continents. *Journal of Vegetation Science*, 15: 295-304.
- 1080 Domingues TF, Meir P, Feldpausch TR, et al. 2010. Co-limitation of photosynthetic capacity by
1081 nitrogen and phosphorus in West Africa woodlands. *Plant, Cell & Environment* (33): 959-
1082 980.
- 1083 Domingues, T.F., Berry, J.A., Martinelli, L.A., Ometto, J.P., Ehleringer, J.R. 2005.
1084 Parameterization of Canopy Structure and Leaf-Level Gas Exchange for an Eastern
1085 Amazonian Tropical Rain Forest (Tapajós National Forest, Pará, Brazil). *Earth Interactions*
1086 9: EI149.
- 1087 Domingues, T.F., Martinelli, L.A. & Ehleringer, J.R. 2007. Ecophysiological traits of plant
1088 functional groups in forest and pasture ecosystems from eastern Amazônia, Brazil. *Plant*

- 1089 Ecology 193: 101-112.
- 1090 Duarte, L. D., M. B. Carlucci, S. M. Hartz, and V. D. Pillar. 2007. Plant dispersal strategies and
1091 the colonization of Araucaria forest patches in a grassland-forest mosaic. *Journal of*
1092 *Vegetation Science* 18: 847-858.
- 1093 Dunbar-Co, S., M. J. Sporck, and L. Sack. 2009. Leaf Trait Diversification and Design in Seven
1094 Rare Taxa of the Hawaiian Plantago Radiation. *International Journal of Plant Sciences* 170:
1095 61-75.
- 1096 Everwand G, Fry, EL, Eggers T, Manning P. 2014. Seasonal variation in the relationship
1097 between plant traits and grassland carbon and water fluxes. *Ecosystems* 17: 1095-1108.
- 1098 Fagúndez, J. & J. Izco. 2008. Seed morphology of two distinct species of *Erica* L. (Ericaceae).
1099 *Acta Botanica Malacitana* 33: 1-9.
- 1100 Fitter, A. H. and H. J. Peat. 1994. The Ecological Flora Database. *Journal of Ecology* 82: 415-
1101 425.
- 1102 Fonseca, C. R., J. M. Overton, B. Collins, and M. Westoby. 2000. Shifts in trait-combinations
1103 along rainfall and phosphorus gradients. *Journal of Ecology* 88: 964-977.
- 1104 Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K., Lavorel, S., Ansquer,
1105 P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Freitas, H., Golodets, C., Jouany, C., Kigel,
1106 J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M.,
1107 Papanastasis, V.P., Quetier, F., Robson, M., Sternberg, M., Theau, J.P., Thebault, A. &
1108 Zarovali, M. 2009. Leaf traits capture the effects of land use changes and climate on litter
1109 decomposability of grasslands across Europe. *Ecology* 90: 598-611.

- 1110 Frenette-Dussault, C., Shipley, B., Léger, J.F., Meziane, D. & Hingrat, Y. 2012. Functional
1111 structure of an arid steppe plant community reveals similarities with Grime's C-S-R theory.
1112 *Journal of Vegetation Science* 23: 208-222.
- 1113 Freschet, G. T., J. H. C. Cornelissen, R. S. P. van Logtestijn, and R. Aerts. 2010. Evidence of the
1114 'plant economics spectrum' in a subarctic flora. *Journal of Ecology* 98: 362-373.
- 1115 Freschet, G. T., J. H. C. Cornelissen, R. S. P. van Logtestijn, and R. Aerts. 2010. Substantial
1116 nutrient resorption from leaves, stems and roots in a sub-arctic flora: what is the link with
1117 other resource economics traits? *New Phytologist* 186: 879-889.
- 1118 Fry, E.L., Power, S.A. Manning, P. 2014. Trait based classification and manipulation of
1119 functional groups in biodiversity-ecosystem function experiments. *Journal of Vegetation*
1120 *Science*, 25: 248-261.
- 1121 Fyllas, N.M., Patiño, S., Baker, T.R., Bielefeld Nardoto, G., Martinelli, L.A., Quesada, C.A.,
1122 Paiva, R., Schwarz, M., Horna, V., Mercado, L.M., Santos, A., Arroyo, L., Jiménez, E.M.,
1123 Luizão, F.J., Neill, D.A., Silva, N., Prieto, A., Rudas, A., Silveira, M., Vieira, I.C.G., Lopez-
1124 Gonzalez, G., Malhi, Y., Phillips, O.L. & Lloyd, J. 2009. Basin-wide variations in foliar
1125 properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences* 6: 2677-2708.
- 1126 Gallagher RV, MR Leishman. 2012. A global analysis of trait variation and evolution in
1127 climbing plants. *Journal of Biogeography* 39: 1757-1771.
- 1128 Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C.,
1129 Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M.,
1130 Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P.,
1131 Quested, H., Quetier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M.,
1132 Theau, J.P., Thebault, A., Vile, D. & Zarovali, M.P. 2007. Assessing the effects of land-use

- 1133 change on plant traits, communities and ecosystem functioning in grasslands: a standardized
1134 methodology and lessons from an application to 11 European sites. *Annals of Botany* 99:
1135 967-85.
- 1136 Gillison, A. N. and G. Carpenter. 1997. A generic plant functional attribute set and grammar for
1137 dynamic vegetation description and analysis. *Functional Ecology* 11: 775-783.
- 1138 Givnish T.J., R.A. Montgomery and G. Goldstein. 2004. Adaptive radiation of photosynthetic
1139 physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant
1140 compensation points. *American Journal of Botany* 91: 228-246.
- 1141 Green, W. 2009. USDA PLANTS Compilation, version 1, 09-02-02.
1142 (<http://bricol.net/downloads/data/PLANTSdatabase/>) NRCS: The PLANTS Database
1143 (<http://plants.usda.gov>, 1 Feb 2009). National Plant Data Center: Baton Rouge, LA 70874-
1144 74490 USA.
- 1145 Guerin G.R., Wen H. & Lowe A.J. 2012. Leaf morphology shift linked to climate change.
1146 *Biology Letters* 8: 882-886.
- 1147 Gutiérrez AG, & Huth A. 2012. Successional stages of primary temperate rainforests of Chiloé
1148 Island, Chile. *Perspectives in plant ecology, systematics and evolution*. 14: 243-256
- 1149 Guy, A. L., J. M. Mischkolz, and E. G. Lamb. 2013. Limited effects of simulated acidic
1150 deposition on seedling survivorship and root morphology of endemic plant taxa of the
1151 Athabasca Sand Dunes in well watered greenhouse trials. *Botany* 91: 176-181.
- 1152 Han, W. X., J. Y. Fang, D. L. Guo, and Y. Zhang. 2005. Leaf nitrogen and phosphorus
1153 stoichiometry across 753 terrestrial plant species in China. *New Phytologist* 168: 377-385.

- 1154 Hao, G. Y., L. Sack, A. Y. Wang, K. F. Cao, and G. Goldstein. 2010. Differentiation of leaf
1155 water flux and drought tolerance traits in hemiepiphytic and non-hemiepiphytic *Ficus* tree
1156 species. *Functional Ecology* 24: 731-740.
- 1157 He, J. S., L. Wang, D. F. B. Flynn, X. P. Wang, W. H. Ma, and J. Y. Fang. 2008. Leaf nitrogen :
1158 phosphorus stoichiometry across Chinese grassland biomes. *Oecologia* 155: 301-310.
- 1159 He, J. S., Z. H. Wang, X. P. Wang, B. Schmid, W. Y. Zuo, M. Zhou, C. Y. Zheng, M. F. Wang,
1160 and J. Y. Fang. 2006. A test of the generality of leaf trait relationships on the Tibetan Plateau.
1161 *New Phytologist* 170: 835-848.
- 1162 Hickler, T. 1999. Plant functional types and community characteristics along environmental
1163 gradients on Öland's Great Alvar (Sweden) Masters Thesis, University of Lund, Sweden.
- 1164 Hill, M.O., Preston, C.D. & Roy, D.B. (2004) *PLANTATT* - attributes of British and Irish
1165 Plants: status, size, life history, geography and habitats. Huntingdon: Centre for Ecology and
1166 Hydrology.
- 1167 Hoof, J., L. Sack, D. T. Webb, and E. T. Nilsson. 2008. Contrasting structure and function of
1168 pubescent and glabrous varieties of Hawaiian *Metrosideros polymorpha* (Myrtaceae) at high
1169 elevation. *Biotropica* 40: 113-118.
- 1170 Kattge, J., W. Knorr, T. Raddatz, and C. Wirth. 2009. Quantifying photosynthetic capacity and
1171 its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global*
1172 *Change Biology* 15: 976-991.
- 1173 Kazakou, E., D. Vile, B. Shipley, C. Gallet, and E. Garnier. 2006. Co-variations in litter
1174 decomposition, leaf traits and plant growth in species from a Mediterranean old-field
1175 succession. *Functional Ecology* 20: 21-30.

- 1176 Kerkhoff, A. J., W. F. Fagan, J. J. Elser, and B. J. Enquist. 2006. Phylogenetic and growth form
1177 variation in the scaling of nitrogen and phosphorus in the seed plants. *American Naturalist*
1178 168:E103-E122.
- 1179 Kichenin, E., Wardle, D.A., Peltzer, D.A., Morse, C.W. & Freschet, G.T. 2013. Contrasting
1180 effects of plant inter- and intraspecific variation on community-level trait measures along an
1181 environmental gradient. *Functional Ecology* 27: 1254-1261.
- 1182 Kirkup, D., P. Malcolm, G. Christian, and A. Paton. 2005. Towards a digital African Flora.
1183 *Taxon* 54:457-466.
- 1184 Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M.,
1185 Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M.,
1186 Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P.,
1187 Götzenberger, L., Hodgson, J.G., Jackel, A.K., Kühn, I., Kunzmann, D., Ozinga, W.A.,
1188 Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann,
1189 B., Cornelissen, J.H.C., Eriksson, O., Garnier, E. & Peco, B. 2008. The LEDA Traitbase: a
1190 database of life-history traits of the Northwest European flora. *Journal of Ecology* 96: 1266-
1191 1274.
- 1192 Koike, F. 2001. Plant traits as predictors of woody species dominance in climax forest
1193 communities. *Journal of Vegetation Science* 12: 327-336
- 1194 Koike, M. Clout, M. Kawamichi, M. De Poorter and K. Iwatsuki eds. 2006. *Assessment and*
1195 *Control of Biological Invasion Risks*. Cambridge, UK and Shoukadoh Book Sellers, Kyoto,
1196 Japan, and IUCN, Gland, Switzerland.
- 1197 Kraft, N. J. B. and D. D. Ackerly. 2010. Functional trait and phylogenetic tests of community
1198 assembly across spatial scales in an Amazonian forest. *Ecological Monographs* 80: 401-422.

- 1199 Kraft, N. J. B., R. Valencia, and D. Ackerly. 2008. Functional traits and niche-based tree
1200 community assembly in an Amazonian forest. *Science* 322: 580-582.
- 1201 Kühn, I., W. Durka, and S. Klotz. 2004. BiolFlor - a new plant-trait database as a tool for plant
1202 invasion ecology. *Diversity and Distributions* 10: 363-365.
- 1203 Kurokawa, H. and T. Nakashizuka. 2008. Leaf herbivory and decomposability in a Malaysian
1204 tropical rain forest. *Ecology* 89: 2645-2656.
- 1205 Laughlin, D. C., J. J. Leppert, M. M. Moore, and C. H. Sieg. 2010. A multi-trait test of the leaf-
1206 height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional*
1207 *Ecology* 24: 493-501.
- 1208 Laughlin, D.C., P.Z. Fulé, D.W. Huffman, J. Crouse, and E. Laliberte. 2011. Climatic constraints
1209 on trait-based forest assembly. *Journal of Ecology* 99: 1489-1499.
- 1210 Lavergne, S. & Molofsky, J. 2007. Increased genetic variation and evolutionary potential drive
1211 the success of an invasive grass. *Proceedings of the National Academy of Sciences* 104:
1212 3883-3888.
- 1213 Lavergne, S., Muenke, N.J. & Molofsky, J. 2010. Genome size reduction can trigger rapid
1214 phenotypic evolution in invasive plants. *Annals of Botany* 105: 109-116.
- 1215 Louault, F., V. D. Pillar, J. Aufrere, E. Garnier, and J. F. Soussana. 2005. Plant traits and
1216 functional types in response to reduced disturbance in a semi-natural grassland. *Journal of*
1217 *Vegetation Science* 16: 151-160.
- 1218 Loveys, B. R., L. J. Atkinson, D. J. Sherlock, R. L. Roberts, A. H. Fitter, and O. K. Atkin. 2003.
1219 Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast-
1220 and slow-growing plant species. *Global Change Biology* 9: 895-91.
- 1221 Malhado, A.C.M., Malhi, Y., Whittaker, R.J., Ladle, R.J., ter Steege, H., Phillips, O.L., Butt, N.,

- 1222 Aragão, L.E.O.C., Quesada, C.A., Araujo-Murakami, A., Arroyo, L., Peacock, J., Lopez-
1223 Gonzalez, G., Baker, T.R., Anderson, L.O., Almeida, S., Higuchi, N., Killeen, T.J.,
1224 Monteagudo, A., Neill, D., Pitman, N., Prieto, A., Salomão, R.P., Vásquez-Martínez, R. &
1225 Laurance, W.F. 2009. Spatial trends in leaf size of Amazonian rainforest trees.
1226 *Biogeosciences* 6: 1563-1576.
- 1227 Manning, P., Houston, K. & Evans, T. 2009. Shifts in seed size across experimental nitrogen
1228 enrichment and plant density gradients. *Basic and Applied Ecology* 10: 300-308.
- 1229 Martin, R. E., G. P. Asner, and L. Sack. 2007. Genetic variation in leaf pigment, optical and
1230 photosynthetic function among diverse phenotypes of *Metrosideros polymorpha* grown in a
1231 common garden. *Oecologia* 151:387-400.
- 1232 McDonald, P. G., C. R. Fonseca, J. M. Overton, and M. Westoby. 2003. Leaf-size divergence
1233 along rainfall and soil-nutrient gradients: is the method of size reduction common among
1234 clades? *Functional Ecology* 17:50-57.
- 1235 Medlyn, B. E. and P. G. Jarvis. 1999. Design and use of a database of model parameters from
1236 elevated [CO₂] experiments. *Ecological Modelling* 124:69-83.
- 1237 Medlyn, B.E., Badeck, F.W., De Pury, D.G.G., Barton, C.V.M., Broadmeadow, M., Ceulemans,
1238 R., De Angelis, P., Forstreuter, M., Jach, M.E., Kellomäki, S., Laitat, E., Marek, M.,
1239 Philippot, S., Rey, A., Strassemeier, J., Laitinen, K., Liozon, R., Portier, B., Roberntz, P.,
1240 Wang, K. & Jstbid, P.G. 1999. Effects of elevated [CO₂] on photosynthesis in European
1241 forest species: a meta-analysis of model parameters. *Plant, Cell & Environment* 22: 1475-
1242 1495.
- 1243 Medlyn, B.E., Barton, C.V.M., Broadmeadow, M.S.J., Ceulemans, R., De Angelis, P.,
1244 Forstreuter, M., Freeman, M., Jackson, S.B., Kellomäki, S., Laitat, E., Rey, A., Roberntz, P.,

- 1245 Sigurdsson, B.D., Strassemeier, J., Wang, K., Curtis, P.S. & Jarvis, P.G. 2001. Stomatal
1246 conductance of forest species after long-term exposure to elevated CO₂ concentration: a
1247 synthesis. *New Phytologist* 149: 247-264.
- 1248 Meir, P. & Levy, P. E. 2007. Photosynthetic parameters from two contrasting woody vegetation
1249 types in West Africa. *Plant Ecology* 192: 277-287.
- 1250 Meir, P., Kruijt, B., Broadmeadow, M., Kull, O., Carswell, F. & Nobre, A. 2002. Acclimation of
1251 photosynthetic capacity to irradiance in tree canopies in relation to leaf nitrogen
1252 concentration and leaf mass per unit area. *Plant, Cell and Environment*. 25: 343-357.
- 1253 Mencuccini, M., 2003. The ecological significance of long distance water transport: short-term
1254 regulation and long-term acclimation across plant growth forms. *Plant, Cell and*
1255 *Environment*, 26: 163-182.
- 1256 Meng, T., Wang, H., Harrison, S.P., Prentice, I., Ni, J. & Wang, G. 2015. Responses of leaf traits
1257 to climatic gradients: adaptive variation versus compositional shifts. *Biogeosciences* 12:
1258 5339.
- 1259 Milla, R. & Reich, P.B. 2011. Multi-trait interactions, not phylogeny, fine-tune leaf size
1260 reduction with increasing altitude. *Annals of Botany* 107: 455-465.
- 1261 Minden, V., Andratschke, S., Spalke, J., Timmermann, H. & Kleyer, M. 2012. Plant trait–
1262 environment relationships in salt marshes: Deviations from predictions by ecological
1263 concepts. *Perspectives in Plant Ecology, Evolution and Systematics* 14: 183-192. Mischkolz,
1264 J. M. 2013. Selecting and evaluating native forage mixtures for the mixed grass prairie.
1265 University of Saskatchewan, Saskatoon, SK.

- 1266 Moles, A. T., D. D. Ackerly, C. O. Webb, J. C. Tweddle, J. B. Dickie, A. J. Pitman, and M.
1267 Westoby. 2005. Factors that shape seed mass evolution. *Proceedings of the National*
1268 *Academy of Sciences of the United States of America* 102: 10540-10544.
- 1269 Moles, A. T., D. S. Falster, M. R. Leishman, and M. Westoby. 2004. Small-seeded species
1270 produce more seeds per square metre of canopy per year, but not per individual per lifetime.
1271 *Journal of Ecology* 92: 384-396.
- 1272 Moretti, M. & Legg, C. 2009. Combining plant and animal traits to assess community functional
1273 responses to disturbance. *Ecography* 32: 299-309.
- 1274 Muller, S. C., G. E. Overbeck, J. Pfadenhauer, and V. D. Pillar. 2007. Plant functional types of
1275 woody species related to fire disturbance in forest-grassland ecotones. *Plant Ecology* 189: 1-
1276 14.
- 1277 Nakahashi, C. D., K. Frole, and L. Sack. 2005. Bacterial leaf nodule symbiosis in *Ardisia*
1278 (*Myrsinaceae*): Does it contribute to seedling growth capacity? *Plant Biology* 7: 495-500.
- 1279 Niinemets, U. 1999. Components of leaf dry mass per area - thickness and density - alter leaf
1280 photosynthetic capacity in reverse directions in woody plants. *New Phytologist* 144: 35-47.
- 1281 Niinemets, U. 2001. Global-scale climatic controls of leaf dry mass per area, density, and
1282 thickness in trees and shrubs. *Ecology* 82: 453-469.
- 1283 Ogaya, R. and J. Penuelas. 2003. Comparative field study of *Quercus ilex* and *Phillyrea latifolia*:
1284 photosynthetic response to experimental drought conditions. *Environmental and*
1285 *Experimental Botany* 50:137-148.
- 1286 Ogaya, R. and J. Penuelas. 2006. Contrasting foliar responses to drought in *Quercus ilex* and
1287 *Phillyrea latifolia*. *Biologia Plantarum* 50: 373-382.

- 1288 Ogaya, R. and J. Penuelas. 2007. Tree growth, mortality, and above-ground biomass
1289 accumulation in a holm oak forest under a five-year experimental field drought. *Plant*
1290 *Ecology* 189: 291-299.
- 1291 Ogaya, R. and J. Penuelas. 2008. Changes in leaf delta C-13 and delta N-15 for three
1292 Mediterranean tree species in relation to soil water availability. *Acta Oecologica-*
1293 *International Journal of Ecology* 34:331-338.
- 1294 Ordonez, J. C., P. M. van Bodegom, J. P. M. Witte, R. P. Bartholomeus, H. F. van Dobben, and
1295 R. Aerts. 2010. Leaf habit and woodiness regulate different leaf economy traits at a given
1296 nutrient supply. *Ecology* 91: 3218-3228.
- 1297 Ordonez, J. C., P. M. van Bodegom, J. P. M. Witte, R. P. Bartholomeus, J. R. van Hal, and R.
1298 Aerts. 2010. Plant Strategies in Relation to Resource Supply in Mesic to Wet Environments:
1299 Does Theory Mirror Nature? *American Naturalist* 175: 225-239.
- 1300 Otto, B. 2002. Merkmale von Samen, Früchten, generativen Germinulen und generativen
1301 Diasporen. In: Klotz, S., Kühn, I. & Durka, W. [eds.]: BIOLFLOR - Eine Datenbank zu
1302 biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland.
- 1303 Overbeck, G. E. 2005. Effect of fire on vegetation dynamics and plant types in subtropical
1304 grassland in southern Brazil. Department für Ökologie. PhD Thesis Technische Universität
1305 München, Freising,
- 1306 Overbeck, G. E. and J. Pfadenhauer. 2007. Adaptive strategies in burned subtropical grassland in
1307 southern Brazil. *Flora* 202: 27-49.
- 1308 Pahl, A.T., Kollmann, J., Mayer, A. & Haider, S. 2013. No evidence for local adaptation in an
1309 invasive alien plant: field and greenhouse experiments tracing a colonization sequence.
1310 *Annals of Botany* 112: 1921-1930.

- 1311 Pakeman, R. J., Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson,
1312 O., Golodets, C., Kigel, J., Kleyer, M., Leps, J., Meier, T., Papadimitriou, M., Papanastasis,
1313 V. P., Quested, H., Quetier, F., Rusch, G., Sternberg, M., Theau, J.-P., Thébault, A & Vile,
1314 D. 2008. Impact of abundance weighting on the response of seed traits to climate and land
1315 use. *Journal of Ecology* 96:355-366.
- 1316 Pakeman, R. J., J. Leps, M. Kleyer, S. Lavorel, E. Garnier, and V. Consortium. 2009. Relative
1317 climatic, edaphic and management controls of plant functional trait signatures. *Journal of*
1318 *Vegetation Science* 20: 148-159.
- 1319 Patiño, S., Lloyd, J., Paiva, R., Baker, T.R., Quesada, C.A., Mercado, L.M., Schmerler, J.,
1320 Schwarz, M., Santos, A.J.B., Aguilar, A., Czimczik, C.I., Gallo, J., Horna, V., Hoyos, E.J.,
1321 Jimenez, E.M., Palomino, W., Peacock, J., Peña-Cruz, A., Sarmiento, C., Sota, A., Turriago,
1322 J.D., Villanueva, B., Vitzthum, P., Alvarez, E., Arroyo, L., Baraloto, C., Bonal, D., Chave, J.,
1323 Costa, A.C.L., Herrera, R., Higuchi, N., Killeen, T., Leal, E., Luizão, F., Meir, P.,
1324 Monteagudo, A., Neil, D., Núñez-Vargas, P., Peñuela, M.C., Pitman, N., Priante Filho, N.,
1325 Prieto, A., Panfil, S.N., Rudas, A., Salomão, R., Silva, N., Silveira, M., Soares deAlmeida,
1326 S., Torres-Lezama, A., Vásquez-Martínez, R., Vieira, I., Malhi, Y. & Phillips, O.L. 2009.
1327 Branch xylem density variations across the Amazon Basin. *Biogeosciences* 6: 545-568.
- 1328 Paula, S. and J. G. Pausas. 2008. Burning seeds: germinative response to heat treatments in
1329 relation to resprouting ability. *Journal of Ecology* 96: 543-552.
- 1330 Paula, S., M. Arianoutsou, D. Kazanis, Ç. Tavsanoğlu, F. Lloret, C. Buhk, F. Ojeda, B. Luna, J.
1331 M. Moreno, A. Rodrigo, J. M. Espelta, S. Palacio, B. Fernández-Santos, P. M. Fernandes,
1332 and J. G. Pausas. 2009. Fire-related traits for plant species of the Mediterranean Basin.
1333 *Ecology* 90: 1420.

- 1334 Peco B., de Pablos I., Traba J. , & Levassor C. (2005) The effect of grazing abandonment on
1335 species composition and functional traits: the case of dehesa *Basic and Applied Ecology*, 6:
1336 175-183
- 1337 Penuelas, J., J. Sardans, J. Llusia, S. Owen, J. Carnicer, T. W. Giambelluca, E. L. Rezende, M.
1338 Waite, and Ü. Niinemets. 2010. Faster returns on "leaf economics" and different
1339 biogeochemical niche in invasive compared with native plant species. *Global Change*
1340 *Biology* 16: 2171-2185.
- 1341 Penuelas, J., J. Sardans, J. Llusia, S. Owen, J. Silva, and Ü. Niinemets. 2010. Higher allocation
1342 to low cost chemical defenses in invasive species of Hawaii. *Journal of Chemical Ecology*
1343 36: 1255-1270.
- 1344 Pierce, S., Brusa G., Sartori M. & Cerabolini B.E.L. 2012. Combined use of leaf size and
1345 economics traits allows direct comparison of hydrophyte and terrestrial herbaceous adaptive
1346 strategies. *Annals of Botany* 109: 1047-1053
- 1347 Pierce, S., Brusa G., Vagge I. & Cerabolini B.E.L. 2013. Allocating CSR plant functional types:
1348 the use of leaf economics and size traits to classify woody and herbaceous vascular plants.
1349 *Functional Ecology* 27:1002-1010.
- 1350 Pierce, S., Ceriani R.M., De Andreis R., Luzzaro A. & Cerabolini B. 2007. The leaf economics
1351 spectrum of Poaceae reflects variation in survival strategies. *Plant Biosystems* 141: 337-343.
- 1352 Pierce, S., Luzzaro A., Caccianiga M., Ceriani R.M. & Cerabolini B. 2007. Disturbance is the
1353 principal α -scale filter determining niche differentiation, coexistence and biodiversity in an
1354 alpine community. *Journal of Ecology* 95: 698-706.
- 1355 Pillar, V. D. and E. E. Sosinski. 2003. An improved method for searching plant functional types
1356 by numerical analysis. *Journal of Vegetation Science* 14: 323-332.

- 1357 Poorter, L. 2009. Leaf traits show different relationships with shade tolerance in moist versus dry
1358 tropical forests. *New Phytologist* 181: 890-900.
- 1359 Poorter, L. and F. Bongers. 2006. Leaf traits are good predictors of plant performance across 53
1360 rain forest species. *Ecology* 87: 1733-1743.
- 1361 Poschlod, P., M. Kleyer, A. K. Jackel, A. Dannemann, and O. Tackenberg. 2003. BIOPOP - a
1362 database of plant traits and Internet application for nature conservation. *Folia Geobotanica*
1363 38: 263-271.
- 1364 Powers, J.S. and Tiffin, P. 2012. Plant functional type classifications in tropical dry forests in
1365 Costa Rica: leaf habit versus taxonomic approaches. *Functional Ecology*, 24: 927–936.
- 1366 Prentice, I.C., Meng, T., Wang, H., Harrison, S.P., Ni, J., Wang, G., 2011. Evidence for a
1367 universal scaling relationship of leaf CO₂ drawdown along a moisture gradient. *New*
1368 *Phytologist* 190: 169–180
- 1369 Preston, K. A., W. K. Cornwell, and J. L. DeNoyer. 2006. Wood density and vessel traits as
1370 distinct correlates of ecological strategy in 51 California coast range angiosperms. *New*
1371 *Phytologist* 170: 807-818.
- 1372 Price, C.A. and B.J. Enquist. Scaling of mass and morphology in Dicotyledonous leaves: an
1373 extension of the WBE model. 2007. *Ecology* 88: 1132–1141.
- 1374 Price, C.A., B.J. Enquist and V.M. Savage. A general model for allometric covariation in
1375 botanical form and function. 2007. *Proceedings of the National Academy of Sciences* 104:
1376 13204-13209.
- 1377 Pyankov, V. I., A. V. Kondratchuk, and B. Shipley. 1999. Leaf structure and specific leaf mass:
1378 the alpine desert plants of the Eastern Pamirs, Tadjikistan. *New Phytologist* 143:131-142.

- 1379 Quero, J. L., R. Villar, T. Maranon, R. Zamora, D. Vega, and L. Sack. 2008. Relating leaf
1380 photosynthetic rate to whole-plant growth: drought and shade effects on seedlings of four
1381 *Quercus* species. *Functional Plant Biology* 35:725-737.
- 1382 Quested, H. M., J. H. C. Cornelissen, M. C. Press, T. V. Callaghan, R. Aerts, F. Trosien, P.
1383 Riemann, D. Gwynn-Jones, A. Kondratchuk, and S. E. Jonasson. 2003. Decomposition of
1384 sub-arctic plants with differing nitrogen economies: A functional role for hemiparasites.
1385 *Ecology* 84: 3209-3221.
- 1386 Reich, P. B., J. Oleksyn, and I. J. Wright. 2009. Leaf phosphorus influences the photosynthesis-
1387 nitrogen relation: a cross-biome analysis of 314 species. *Oecologia* 160:207-212.
- 1388 Reich, P. B., M. G. Tjoelker, K. S. Pregitzer, I. J. Wright, J. Oleksyn, and J. L. Machado. 2008.
1389 Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. *Ecology*
1390 *Letters* 11:793-801.
- 1391 Reinhard Schober (1996) Ertragstabellen wichtiger Baumarten bei verschiedener Durchforstung.
1392 Sauerlaenders, Frankfurt Main, 4th Edition.
- 1393 Royal Botanical Gardens KEW. 2008. Seed Information Database (SID). Version 7.1. Available
1394 from: <http://data.kew.org/sid/> (May 2008).
- 1395 Royal Botanical Gardens KEW. 2008. Seed Information Database (SID). Version 7.1. Available
1396 from: <http://data.kew.org/sid/> (May 2011).
- 1397 Sack, L. 2004. Responses of temperate woody seedlings to shade and drought: do trade-offs limit
1398 potential niche differentiation? *Oikos* 107: 110-127.
- 1399 Sack, L. and K. Frole. 2006. Leaf structural diversity is related to hydraulic capacity in tropical
1400 rain forest trees. *Ecology* 87: 483-491.

- 1401 Sack, L., P. D. Cowan, N. Jaikumar, and N. M. Holbrook. 2003. The 'hydrology' of leaves: co-
1402 ordination of structure and function in temperate woody species. *Plant Cell and Environment*
1403 26: 1343-1356.
- 1404 Sack, L., P. J. Melcher, W. H. Liu, E. Middleton, and T. Pardee. 2006. How strong is
1405 intracanalopy leaf plasticity in temperate deciduous trees? *American Journal of Botany* 93:
1406 829-839.
- 1407 Sanda et al. (2003): Sanda V., Bită-Nicolae C.D. & Barabă N. 2003. The flora of spontane and
1408 cultivated cormophytes from Romania. Editura "Ion Borcea", Bacău, 316 p (in Romanian).
- 1409 Sardans, J., J. Penuelas, and R. Ogaya. 2008. Drought-induced changes in C and N stoichiometry
1410 in a *Quercus ilex* Mediterranean forest. *Forest Science* 54: 513-522.
- 1411 Sardans, J., J. Penuelas, P. Prieto, and M. Estiarte. 2008. Changes in Ca, Fe, Mg, Mo, Na, and S
1412 content in a Mediterranean shrubland under warming and drought. *Journal of Geophysical*
1413 *Research* 113:G3.
- 1414 Scherer-Lorenzen, M., Schulze, E.-D., Don, A., Schumacher, J. & Weller, E. 2007. Exploring the
1415 functional significance of forest diversity: A new long-term experiment with temperate tree
1416 species (BIOTREE). *Perspectives in Plant Ecology, Evolution and Systematics* 9: 53-70.
- 1417 Schurr, F.M., Midgley, G.F., Rebelo, A.G., Reeves, G., Poschlod, P. & Higgins, S.I. 2007. Global
1418 Ecology and Biogeography 16: 449-459.
- 1419 Schweingruber, F.H., Landolt, W. 2005. The Xylem Database. Swiss Federal Research Institute
1420 WSL.
- 1421 Schweingruber, F.H., Poschlod, P. 2005. Growth rings in herbs and shrubs: Life span, age
1422 determination and stem anatomy. *Forest, Snow and Landscape Research* 79: 195-415.

- 1423 Scoffoni, C., A. Pou, K. Aasamaa, and L. Sack. 2008. The rapid light response of leaf hydraulic
1424 conductance: new evidence from two experimental methods. *Plant Cell and Environment*
1425 31:1803-1812.
- 1426 Shiodera, S., J. S. Rahajoe, and T. Kohyama. 2008. Variation in longevity and traits of leaves
1427 among co-occurring understorey plants in a tropical montane forest. *Journal of Tropical*
1428 *Ecology* 24:121-133.
- 1429 Shipley, B. 1995. Structured Interspecific Determinants of Specific Leaf-Area in 34 Species of
1430 Herbaceous Angiosperms. *Functional Ecology* 9: 312-319.
- 1431 Shipley, B. and M. J. Lechowicz. 2000. The functional co-ordination of leaf morphology,
1432 nitrogen concentration, and gas exchange in 40 wetland species. *Ecoscience* 7: 183-194.
- 1433 Shipley, B. and M. Parent. 1991. Germination Responses of 64 Wetland Species in Relation to
1434 Seed Size, Minimum Time to Reproduction and Seedling Relative Growth-Rate. *Functional*
1435 *Ecology* 5: 111-118.
- 1436 Shipley, B. and T. T. Vu. 2002. Dry matter content as a measure of dry matter concentration in
1437 plants and their parts. *New Phytologist* 153: 359-364.
- 1438 Sophie Gachet, Errol Véla, Thierry Tatoni. 2005. BASECO: a floristic and ecological database
1439 of Mediterranean French flora. *Biodiversity and Conservation* 14: 1023-1034.
- 1440 Spasojevic, M. J. and K. N. Suding. 2012. Inferring community assembly mechanisms from
1441 functional diversity patterns: the importance of multiple assembly processes. *Journal of*
1442 *Ecology* 100: 652-661.
- 1443 Swaine, E. K. 2007. Ecological and evolutionary drivers of plant community assembly in a
1444 Bornean rain forest. PhD Thesis, University of Aberdeen, Aberdeen.

- 1445 Vergutz, L., Manzoni, S., Porporato, A., Novais, R. F., and Jackson, R. B. 2012. Global
1446 resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial
1447 plants. *Ecological Monographs* 82: 205-220.
- 1448 Vergutz, L., S. Manzoni, A. Porporato, R.F. Novais, and R.B. Jackson. 2012. A Global Database
1449 of Carbon and Nutrient Concentrations of Green and Senesced Leaves. Data set available on-
1450 line [<http://daac.ornl.gov>].
- 1451 Vile, D. 2005. Significations fonctionnelle et ecologique des traits des especes vegetales:
1452 exemple dans une succession post-cultural mediterraneenne et generalisations, PhD Thesis.
- 1453 Von Holle, B. and D. Simberloff. 2004. Testing Fox's assembly rule: Does plant invasion depend
1454 on recipient community structure? *Oikos* 105:551-563.
- 1455 Waite, M. and L. Sack. 2010. How does moss photosynthesis relate to leaf and canopy structure?
1456 Trait relationships for 10 Hawaiian species of contrasting light habitats. *New Phytologist*
1457 185:156-172.
- 1458 Wenxuan Han, Yahan Chen, Fang-Jie Zhao, Luying Tang, Rongfeng Jiang and Fusuo Zhang.
1459 2011. Floral, climatic and soil pH controls on leaf ash content in China's terrestrial plants.
1460 *Global Ecology and Biogeography* 21: 376-382.
- 1461 Williams, M., Y.E. Shimabokuro and E.B. Rastetter. 2012. LBA-ECO CD-09 Soil and
1462 Vegetation Characteristics, Tapajos National Forest, Brazil. Data set. Available on-line
1463 [<http://daac.ornl.gov>].
- 1464 Willis, C. G., M. Halina, C. Lehman, P. B. Reich, A. Keen, S. McCarthy, and J. Cavender-Bares.
1465 2010. Phylogenetic community structure in Minnesota oak savanna is influenced by spatial
1466 extent and environmental variation. *Ecography* 33: 565-577.

- 1467 Wilson, K, D. Baldocchi, and P. Hanson. 2000. Spatial and seasonal variability of photosynthetic
1468 parameters and their relationship to leaf nitrogen in a deciduous forest. *Tree Physiology* 20:
1469 565–578
- 1470 Wirth, C. and J. W. Lichstein. 2009. The Imprint of Species Turnover on Old-Growth Forest
1471 Carbon Balances - Insights From a Trait-Based Model of Forest Dynamics. In C. Wirth, G.
1472 Gleixner, and M. Heimann, editors. *Old-Growth Forests: Function, Fate, and Value*.
1473 Springer: pages 81-113.
- 1474 Wohlfahrt, G., Bahn, M., Haubner, E., Horak, I., Michaeler, W., Rottmar, K., Tappeiner, U. &
1475 Cernusca, A. 1999. Inter-specific variation of the biochemical limitation to photosynthesis
1476 and related leaf traits of 30 species from mountain grassland ecosystems under different land
1477 use. *Plant, Cell & Environment* 22: 1281-1296. Wright JP, Sutton-Grier A. 2012. Does the
1478 leaf economic spectrum hold within local species pools across varying environmental
1479 conditions? *Functional Ecology* 26: 1390-1398.
- 1480 Wright, I. J., P. B. Reich, O. K. Atkin, C. H. Lusk, M. G. Tjoelker, and M. Westoby. 2006.
1481 Irradiance, temperature and rainfall influence leaf dark respiration in woody plants: evidence
1482 from comparisons across 20 sites. *New Phytologist* 169: 309-319.
- 1483 Wright, I.J., Ackerly, D.D., Bongers, F., Harms, K.E., Ibarra-Manriquez, G., Martinez-Ramos,
1484 M., Mazer, S.J., Muller-Landau, H.C., Paz, H., Pitman, N.C., Poorter, L., Silman, M.R.,
1485 Vriesendorp, C.F., Webb, C.O., Westoby, M. & Wright, S.J. 2007. Relationships among
1486 ecologically important dimensions of plant trait variation in seven neotropical forests. *Annals*
1487 *of Botany* 99: 1003-15.
- 1488 Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares,
1489 J., Chapin, T., Cornelissen, J.H., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J.,

- 1490 Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L.,
1491 Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet,
1492 C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. .2004. The worldwide leaf
1493 economics spectrum. *Nature* 428: 821-7.
- 1494 Wright, S.J., Kitajima, K., Kraft, N.J., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R.,
1495 Dalling, J.W., Davies, S.J., Diaz, S., Engelbrecht, B.M., Harms, K.E., Hubbell, S.P., Marks,
1496 C.O., Ruiz-Jaen, M.C., Salvador, C.M. & Zanne, A.E. 2010. Functional traits and the
1497 growth-mortality trade-off in tropical trees. *Ecology* 91: 3664-74.
- 1498 Xu, L. K. and D. D. Baldocchi. 2003. Seasonal trends in photosynthetic parameters and stomatal
1499 conductance of blue oak (*Quercus douglasii*) under prolonged summer drought and high
1500 temperature. *Tree Physiology* 23: 865-877.
- 1501 Yguel B., Bailey R., Tosh N.D., Vialatte A., Vasseur C., Vitrac X., Jean F. & Prinzing A. 2011.
1502 Phytophagy on phylogenetically isolated trees: why hosts should escape their relatives.
1503 *Ecology Letters* 14: 1117-1124.
- 1504 Zanne, A. E., G. Lopez-Gonzalez, D. A. Coomes, J. Ilic, S. Jansen, S. L. Lewis, R. B. Miller, N.
1505 G. Swenson, M. C. Wiemann, and J. Chave. 2009 Global wood density database. Dryad
1506 identifier: <http://hdl.handle.net/10255/dryad.10235>.
- 1507 Zheng, W. 1983. *Silva Sinica*: Volume 1-4. China Forestry Publishing House, Beijing.
1508

27 May 2018

Dear Dr. Penuelas,

Thank you for your effort handling our manuscript. We appreciate the thoughtful and constructive reviews that we received. We have now prepared a revised submission that addresses all of the reviewer points. In particular, we have:

- Removed the ECBilt-CLIO model from the paper, per advice from Reviewer #1;
- Redrawn most figures for enhanced clarity, with larger font sizes and legends;
- Better explained the biases inherent to the data, and justified our choices to minimize them, throughout the text;
- Extended discussion of megafauna and non-climate factors in driving our results.

A detailed response to the review comments follows below, with our responses in **boldface** type. We hope that our changes will be sufficient to render the manuscript acceptable for publication. Thank you again for your consideration.

Sincerely,
Benjamin Blonder, on behalf of my co-authors

For Review Only

Reviewer: 1

Comments to the Author

This study uses what appear to be the best available plant assemblage and climate reconstruction data to test whether palaeoclimate is 1) important in explaining contemporary plant community functional means and diversity, and 2) infers from those influences whether processes of plant functional community turnover are fast or slow.

Overall the study represents a thorough, comprehensive, and well-reasoned undertaking of an important question, which stands to influence a broad variety of global change topics. There are very few points on which I think the study could improve, although some recommendations are made below, including around breadth of explanations and reference to the literature, as well as points around ease of understanding and presentation of figures. A few issues around description of results require definite correction before publication can be considered.

We thank the reviewer for their interest in our work.

Specific Comments on Manuscript

Introduction –

Paragraphs 1 – 3: Suitably general in their statements, but literature cited is very plant-dominated, with reference to few other taxa. Discussion that this study is specific to plant FM & FD comes is not yet introduced. Some additional examples from other taxa would help reflect the generality of these statements – in particular I raise a point w.r.t. the discussion (see below) regarding late-Quaternary loss of megafauna, which may be a suitable topic to cite here. Alternatively, the authors may wish to make it more explicit that this study and the cited works are principally in relation to plant communities earlier on than in this section.

We regret this lack of clarity. We have rewritten the first few paragraphs of the introduction to clarify that our results – and cited literature – are meant to primarily apply to plant assemblages.

Lines 104 – 129: I would like to commend the authors on the quality and clarity of writing in this section.

We appreciate this feedback.

Fig. 1: This explanatory figure was greatly appreciated during reading, however some minor changes to improve interpretability would be:

- The green 'tree symbols' differ in their opacity (and shape). Differing their colour (yellow, blue, red?) without differences in their opacities would ease interpretation in my opinion.

We appreciate the suggestion, but prefer to keep the existing scheme. While we agree that high contrast could be provided by using differing colors, we believe that changing opacity will reproduce better in black & white printouts of the figure. The differing shapes also already provide contrast. We are open to changing this upon further editorial advice.

- The charts illustrating +ve or -ve effects on FM & FD would be more easily understood if the graphs for FM and FD were entirely separated with white space between plot panels. Additionally, the '+' and '-' symbols would be better placed outside the plot-axis areas. I would also like to see the font size increased, and the use of annotation lines to allow for horizontal text would improve readability.

We have increased the white space between the right panels and the left panels. We have used some of this space to move the +/- symbols to a clearer position, and also added a 0 symbol. We have also increased the font size, but are not sure what is meant by annotation lines.

- The legend being above the figure (true also elsewhere) is atypical, but I expect this would be changed following publisher's formatting.

We believe that this placement of the legend minimizes unused space in the figure, as some of this vertical header is needed to label the rightmost panels of the figure.

Lines 144-161: Again, the clarity of the explanations here should be commended.

Thank you!

Line 170 (& elsewhere): I would recommend the authors try and more clearly distinguish their uses of 'Ka' depending on whether it is being used to mean 'thousands of years ago' or simply 'thousand years' – i.e. a time before present or just a period of time. Whilst I appreciate there is no uniform consensus on this matter, in this study 'Ka' seems to be used to mean both, and then elsewhere in the manuscript 'Kyr' is also used (see lines 298 & surrounding). The reader's understanding would be better served by use of 'kya' for 'thousand years ago' and 'kyr' for 'thousand years', or similar distinguishing units meaning 'before present' and as a period unit of time. Additionally, I would highlight that the 'K'(kilo) shouldn't be capitalised.

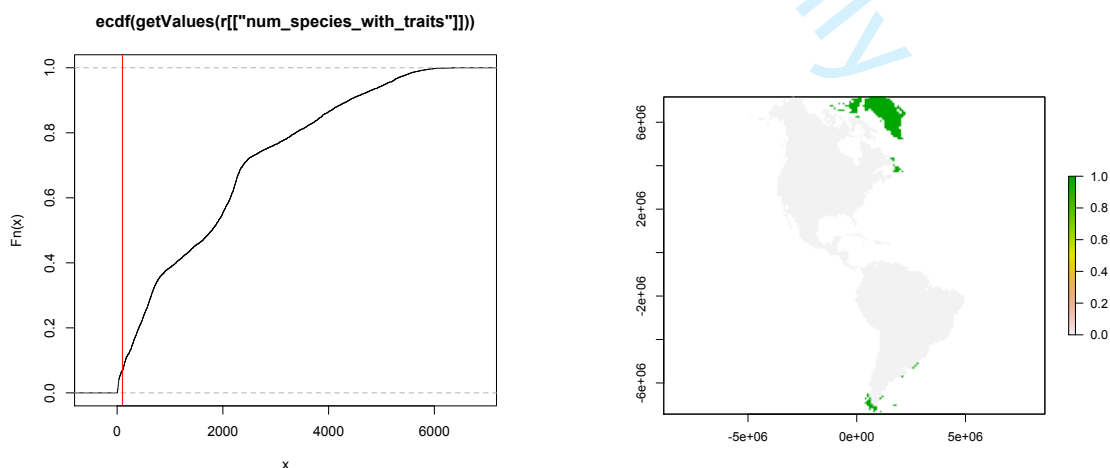
We have standardized on lower case capitalization in all figures and the text. We have also carefully checked all uses of ka and kyr and found only one instance where the term was not used correctly. The text is now fixed.

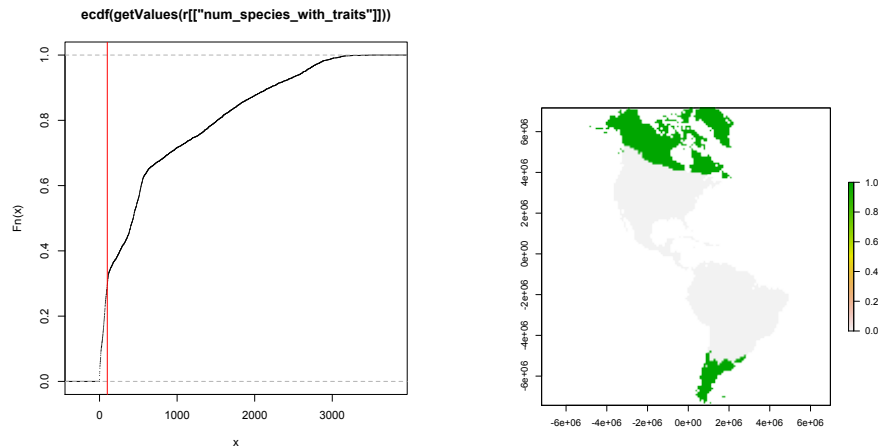
Methods –

Line 208: 'arbitrarily' raises concerns here as a phrase. Can some context be given for this value of 100? How it relates to mean or median species richness across all the cells (and a measure of spread around such a figure), would be informative. I trust this choice of < 100 not to be a problem, but some comparative context would help in the explanation of this cut-off.

The reviewer is correct that the cut-off was chosen to be small, and to remove unwanted cells with poor data coverage or current permanent ice cover. It represents the 7% quantile of richness for the 'all' species case and the 29% for the 'woody' species case. We simply do not feel comfortable estimating trait distributions with a very low number of species with trait coverage and prefer to lose spatial coverage rather than proceed with biased estimates.

The empirical cumulative distribution function of richness for the 'all' species case is shown below. The vertical red line indicates the chosen cut-off. The cells that are removed by the analysis are shown in green in the rightmost map. (Top row, all species; bottom row, woody species only).





We have clarified the text to reflect the rationale for this choice.

We do want to note that the woody maps and results are slightly different in our revised submission compared to our original submission. In the original, we gap-filled traits for all species using data for only the woody subset, then applied these to all species for the functional composition estimates. We have decided it is better (and more consistent with how we wrote the methods originally) to gap-fill traits for all species, then apply to only species that are classified as woody. The net effect is that the richness per cell in the woody species case decreases (as we are now only including woody species, rather than all species estimated with woody species' traits) and some of the functional composition metrics change slightly. There is however no qualitative change in analysis outcomes, as can be verified by comparing the main text figures in the revised and original submission.

General: I was pleased to see how the authors carried out their testing, in particular the use of residual FD in addition to their initial FD and FM measurements. The justification for their approaches was also eloquently explained.

Thank you!

Fig. 2: Colour bar annotations are difficult to make out – I recommend widening the colour bars, removing or reducing the thick black outline/box, and increasing adjacent font sizes (maybe by reducing decimal place precision).

We have widened the colorbars and reduced the precision of the labels in the legends.

Climate Model: The mismatched MAP values between the HadCM3 and ECBilt-Clio are a little concerning. Do the authors feel comfortable commenting on / assessing which model is likely to be more accurate? If the HadCM3 climate reconstruction is likely superior (lines 525-526 suggest so), I would encourage the authors to cut all analysis and mention of the ECBilt-Clio model, as it is so temporally restricted in comparison.

We believe the HadCM3 model is strictly superior, but originally included the ECBilt-CLIO model based on prior reviewer suggestions. We have now removed it entirely from the analysis.

Line 298 (& 303): Immediate clarity with variation in window sizes depending on reconstruction period, as soon as the window concept is introduced, would be appreciated. The earlier description of the climate models make the mention of this window size on L298 confusing, only for the clarification to come five lines later on L303.

We clarified this paragraph by re-arranging, indicating the normalization approach and the HadCM3 resolution issue earlier on.

312-334 – Notably well written & justified methodology.

Thank you.

352-355 – Citations for all packages would be appropriate (from a cursory check, at least one of the used packages has an easily accessed associated citation).

We have added citations.

Results –

Fig. 3: Same comments as Fig. 2 and other maps – larger colour scale bars, reduce outlining box line weight, increase font size.

We have improved the font size in the legends.

Fig. 4: More care needs to be taken with this figure and its explanation. “Blue lines indicate models using only contemporary <...> orange lines, models using contemporary & palaeo” this account in the legend is directly opposite to the actual illustrated legend / annotation on the graph. The correct colours can be inferred from the results, but this is a problematic error. Additionally, it is not clear to me why the orange line is so limited compared to the blue? The blue line spans the whole length of the X-axis range, whilst the orange stops after only 1 x-axis step. An explanation of this, or correction of the plotting error, is necessary.

We regret the confusion. The color scheme was reversed immediately before submission and we neglected to update the caption. The reviewer is correct that orange reflects contemporary climate variables.

The differences in x-axis range for blue vs. orange is intentional and correct. We have only two contemporary climate axes (temp and precip) while we have many more paleoclimate axes (temp & precip at 0 ka, 1 ka, 2 ka, etc.). Mathematically, the number of PLS components in the model can be up the number of predictor variables (i.e. in the same way that a principal component analysis has as many principal components as input variables). Thus the paleo + contemp model can potentially have many more PLS components than the contemp model. We clarified this by including a sentence on number of variables in the ‘We tested Hypothesis H0’ paragraph.

Additionally, the link to figure panel 3H must be clarified. I think I understand that this is testing prediction of FD, and therefore model evaluation is in the same units as residual-FD (which is shown in 3H). However a cursory reading could lead to thinking that what is being tested is FDres, mapped in fig 3H, rather than FD, mapped in figure 3G.

Overall this crucial figure requires better explanation, framing in terms of Fig 3, and clarification.

We regret this imprecision, which was also caused by a panel reorganization before submission. We now write ‘units of functional diversity (compare to Figure 3G)’.

Discussion –

Overall the discussion is well written and there are next-to-no changes to suggest.

My main comment is around lines 533-542. I think the authors understate the importance of this work in its links to other climate-interacting processes determining plant assemblages. Some reference is made to megafaunal extinctions (Gill et al. 2009), but the phrasing suggests that these processes are separate from the effects of the palaeoclimate. I think that megafauna-mediated effects provide an interesting indirect mechanism for palaeoclimate to influence plant assemblages, and therefore FM & FD, and should be (at least briefly) discussed here.

For example, Pires et al. (2018), Gill (2014), Gill et al. (2012), and Doughty et al. (2009) all demonstrate that the loss of megafauna will influence plant assemblages into the long-term, with examples specifically from the Western Hemisphere and this study’s temporal period. Whilst human activity is undeniably a cause of megafaunal loss, Bartlett et al. (2016) showed that climate also had an important role in the loss of Pleistocene

megafauna – including in the Western Hemisphere. In particular I think it's noteworthy that their study also used what appears to be the same (or a very similar version) of the HadCM3 reconstruction used by the authors of this study.

I think therefore that more can be made of megafaunal extinction or population decline as an additional mechanism behind the effect of palaeoclimate on contemporary functional assemblage. It may even provide insights into when immigration or exclusion are fast or slow processes

I think the authors understate the relevance of their study in terms of its integration with this topic, and think with additional citations (a few of which I have provided here) and at least brief discussion, their findings would be even more impactful than they are currently presented to be.

We thank the reviewer for this point, and agree with it. We have added a new paragraph to discuss indirect effects of climate on species composition in much more depth.

Pires, M. M., Guimarães, P. R., Galetti, M., & Jordano, P. (2018). Pleistocene megafaunal extinctions and the functional loss of long-distance seed-dispersal services. *Ecography*, 41(1), 153-163.

Gill, J. L. (2014). Ecological impacts of the late Quaternary megaherbivore extinctions. *New Phytologist*, 201(4), 1163-1169.

Gill, J. L., Williams, J. W., Jackson, S. T., Donnelly, J. P., & Schellinger, G. C. (2012). Climatic and megaherbivory controls on late-glacial vegetation dynamics: a new, high-resolution, multi-proxy record from Silver Lake, Ohio. *Quaternary Science Reviews*, 34, 66-80.

Bartlett, L. J., Williams, D. R., Prescott, G. W., Balmford, A., Green, R. E., Eriksson, A., ... & Manica, A. (2016). Robustness despite uncertainty: regional climate data reveal the dominant role of humans in explaining global extinctions of Late Quaternary megafauna. *Ecography*, 39(2), 152-161.

Doughty, C. E., Wolf, A., & Malhi, Y. (2013). The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. *Nature Geoscience*, 6(9), 761.

Reviewer: 2

Comments to the Author

Dear authors,

see my comments to the editor and my detailed comments below:

In their manuscript “Late Quaternary climate legacies in contemporary plant functional composition” Blonder et al. show for plants across the Americas that contemporary functional trait composition of assemblages is linked to Paleoclimate indicating that processes reorganizing assemblages have been slower than the changing climate. They test four hypotheses on how past climate, past climate variation and contemporary climate affect contemporary functional trait means and functional diversity. They find that climate closely after the Last Glacial Maximum has left a strong imprint on contemporary functional composition. Results for what mechanisms (slow or fast immigration and/or exclusion) are responsible for the observed patterns were different among the two continents showing the complexity of the processes behind the observed patterns and calling for future analyses based on time series of functional composition.

The manuscript is very well written, the methods are state of the art and well-described, and the results are presented in a nice way and discussed appropriately given the available body of literature. The topic is certainly of interest to a broad community of Macroecologists and beyond and the results are novel (given the functional perspective) and exciting. I therefore recommend considering the paper for publication in *Global Change Biology*. However, I have some concerns about how potential effects of quality issues with the trait and distribution data (which are discussed in the text) on the results are assessed and I suggest to perform rigorous sensitivity analyses. I therefore recommend a “major revision”. Unfortunately the online review system only allows to chose “minor revision without reassessment” and “reject and invite to resubmit”. Since I don’t want to participate in this game of artificially reducing the time from submission to publication, I chose “minor revision”. However, I urge the authors to take my comments seriously.

We thank the reviewer for their interest in our work.

Comments to the authors:

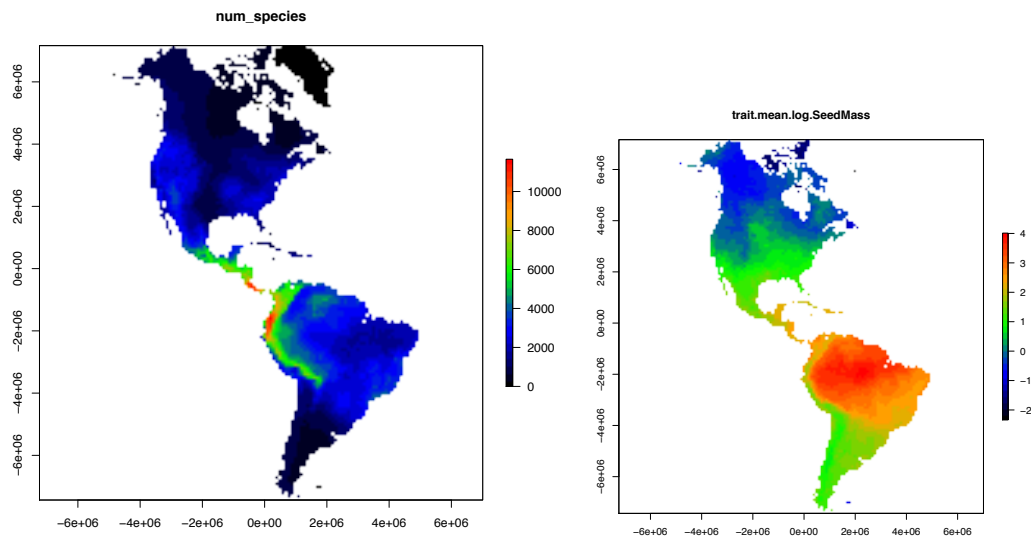
Major points

My only main doubt about this paper concerns if potential biases in the trait and distribution data might have affected the results. The maps of trait means and FD look extremely smooth (Fig. 3), which I would guess is due to the quite low availability of actual trait (a lot imputed) and distribution data (convex hulls sometimes around few occurrences)? Also, some patterns look a bit artificial (almost straight horizontal and vertical lines) in some of the plots (e.g. Fig. 3 G. Functional Diversity and H. FD residual). Can you explain this? I would therefore like to see sensitivity analyses on how gap filling for traits, genus means for species without trait records and species with few distribution records influence the results. It would also be helpful to show spatial coverage patterns for the trait and distribution data.

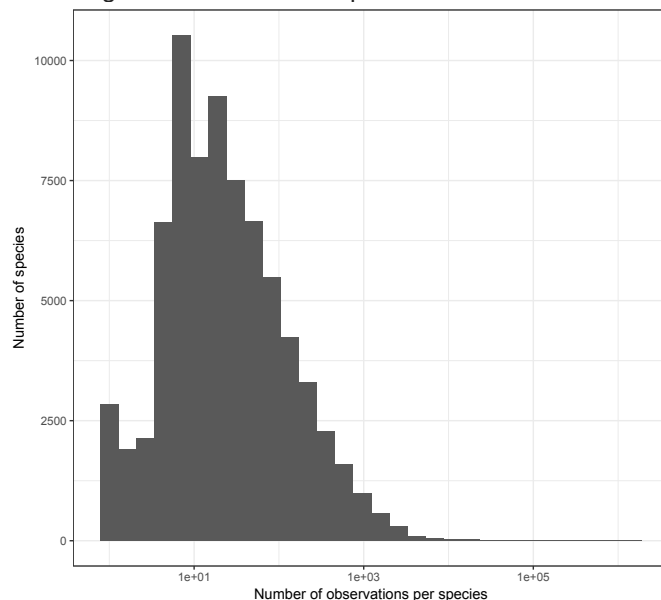
The reviewer is correct in noticing that the distribution data are coarse, and sometimes include what are likely artifacts of the modeling method. Part of this effect comes from the greater quantity of occurrence data available in the United States relative to Canada (the upper horizontal line) and the lower quantity of data available in southern south America (the southern angled line). Some species also may have coastal distributions, which can lead to artifacts in range maps when a convex hull method is used. We acknowledge these issues, but feel that they are inevitable ‘costs’ of a SDM approach that does not calibrate predictions based on contemporary climate data. For example, a MaxEnt type model would produce species distribution (& thus functional diversity) maps without many of these artifacts. The downside is some circularity, as a map of FD produced by calibration on contemporary climate data will surely show that contemporary climate is a good predictor of FD.

In a previous iteration of this manuscript at a different journal, we included MaxEnt type models for the FD calculations. We show a few example figures from this analysis below. While some of these ‘sharp edge’ artifacts are now gone, the overall spatial patterns are often quite similar.

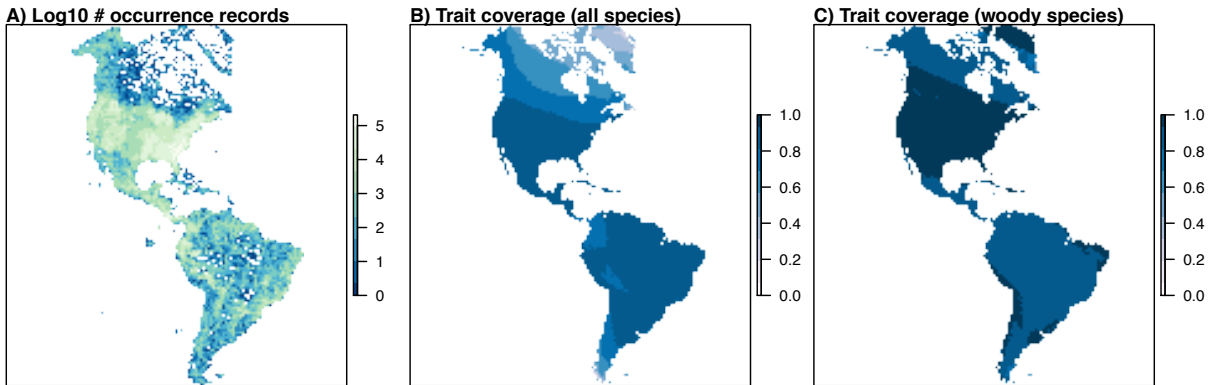
It is also important to remember that the overall analysis is constrained by the spatial resolution of the paleoclimate data, which is at a nominal 2° resolution, but in practice has lower resolution due to the spatial structure of the model. As such, many features in the FD and richness maps are effectively ‘blurred out’ by the PLS analysis. For this reason, we decided against trying to take more complex modeling approaches.



Regarding the data coverage issues (both for species with too few occurrence points, and for species with no trait data), the reviewer has requested sensitivity analyses, or alternate analyses with removing these data points. We have thought long and hard about this issue when preparing this project, and ultimately believe that carrying them out would not be helpful. In the absence of complete data, any methods taken to fill in data will potentially introduce biases – and something as simple as removing data may in fact have a much larger bias than the gap-filling and space-filling methods we have elected to use. In this dataset, 24,042 of the 74,000 species are represented by 10 or fewer observations, and most of these species are tropical – thus, losing these species would represent a very large bias in the dataset. In another in-progress study led by co-author Enquist, it is shown that most of these database-rare species are actually rare and have restricted ranges according to interviews with expert botanists.



Above, histogram of occurrence records per species; below, heatmap of occurrences over space (note the log-scale z axis). Additionally, trait data for 59,423 species out of 74,000 was not available. The trait coverage is higher in tropical regions.



Omitting cells with low trait coverage would also introduce a large spatial bias. Our resampling approach is, we believe, the best way to deal with the impacts of low trait coverage on functional diversity.

We therefore feel that the approach we have taken is the least bad of all the bad options, given the currently available data resources for plant macroecology. Removing rare species, and removing species without trait data would lead to highly sparse and biased estimates. Our trait maps and richness maps are approximately congruent with other recent mapping efforts (e.g. Jetz's late-2000s work, or Butler et al. in PNAS this year, which the lead author is a co-author on), but are more appropriate for this application because of the lack of circularity.

We hope that this extended response is convincing to the reviewer. We have clarified the methods text to reflect the bulk of these points. We have included the trait coverage and occurrence point coverage figures in the resubmission.

I could imagine that due to the smooth spatial patterns in the response variables (Trait means and FD metrics) the spatially smooth paleo climate data performs better than the high resolution and spatially more heterogeneous contemporary climate data. Maybe the different resolutions and methods how contemporary climate and paleoclimate are derived are partly responsible for the findings (btw. Chelsa now also offers LGM climate at high resolution). It is striking that contemporary and Paleoclimate were not strongly correlated (lines 289-290). Maybe the coarser resolution of the Paleoclimate layer fits better to the coarse spatial scale of the distribution data?

We agree that methodological differences in how the paleoclimate and contemporary climate datasets are created could drive some of the findings. We appreciate the suggestion for the higher resolution CHELSA dataset, but for this application we would need that high resolution at every time point back to 120 ka, which is to our understanding not yet (or perhaps not ever) feasible.

While the reviewer argues that contemporary and paleoclimate axes are not strongly correlated, we believe that our supplementary figure shows otherwise, also the definition of 'strongly' is certainly debatable. Rather than report the Pearson correlation between these maps, which could be high even if the actual values are down or up biased, we report the mean absolute deviation between them. These values are less than 0.5 standard deviations throughout the Holocene, which we think reflects strong correlation, and then diverge during the late Pleistocene, as expected. We have clarified the main text to better explain when and when not there is evidence for matching between these variables.

We also note that based on feedback from the first reviewer, we now no longer include the ECBilt-CLIO analyses in the paper.

Minor points:

Line 63: delete one of the two "to"s

Fixed.

Line 79: rather “little” than “less”?

Changed.

Line 81: „paleoclimate has structured contemporary“ sounds too obvious to me. The question rather is, how much of it is still visible, right?

We prefer to keep this phrase as-is – a great deal of species distribution modeling assumes that there is no influence of paleoclimate on species ranges – so while we agree that it is obvious paleoclimate should matter, we do not think everyone would agree with this statement.

Line 82: Also secondary effects due to climate change like changes in sea levels (See literature examples for islands)

We agree this is reasonable, but our downstream analyses do not have the ability to account for variation in sea level. We now write ‘climate has directly & indirectly’ as a compromise.

Lines 83-85: Is this something tackled here?

We believe it is – all of our conceptual models focus on fast vs slow (i.e. lagged) dynamics of organisms. To clarify we now write, “It has been unclear how these paleoclimate effects on species composition translate to differences in functional composition, because even species assemblages in disequilibrium with contemporary climate may have equilibrium functional relationships with contemporary climate”

Lines 101: Do you want to state that the influence is still visible?

To clarify, we write ‘contemporary functional composition’ instead of ‘functional composition’.

Line 145 “and also”?

We clarified conditional phrasing throughout this paragraph.

Line 170: “(120 Ka [thousands of years ago])” Not clear to me

Ka is meant to define ‘thousand years ago’. We removed this definition as we think it is well-understood by most readers.

Line 185: What does “collinear observations” mean?

Collinear is a standard mathematical term referring to points that fall on the same line (<https://en.wikipedia.org/wiki/Collinearity>). We clarify by writing ‘observations’ now as ‘observation points’.

Line 235-238: Species richness

We do not understand what change we should make to the text here, as species richness is already used throughout the sentence. We did find one ‘richness’ and changed it to ‘species richness’ on the following line.

Line 307 “type type” -> “type”

Fixed.

Line 454: “appears”

Fixed.

Line 455: Why “additionally”? Aren’t the previous sentences saying the same?

We removed the ‘additionally’.

Line 465: “ , ,”

Fixed.

Figure S3 I think you could remove white space and make the maps larger if you only show one legend for all of them and change the location of the titles.

We prefer to keep the legend on each panel to enable easy comparison of colors. However we have moved the titles to reduce white space.

For Review Only

Reviewer: 3

Comments to the Author

It was a real pleasure to read this manuscript. The scope of the analysis is very impressive, the analytical methods appear well chosen and meticulously applied. Moreover the detection of lag effects on contemporary trait composition is of great interest because it means that the pool exposed to future global change and that deliver trait-associated ecosystem functions may exhibit on-going slow dynamics as it continues to equilibrate to current climate space.

We than the reviewer for their interest.

My only question centres on their assumption that the traits selected are strong carriers of the climate signal. For example Ordoñez et al (2009) report weak relationships between MAT, MAP and SLA, leaf N (mass and area basis in their Fig 2) but inferred clear interactions and main effects of soil nutrients. Also Wright et al (2005) reported weak correlations but did conclude that they were strong enough to show a biogeographic influence of climate.

Thus if the traits selected are also strongly related to other abiotic conditions then it seems possible that the strong correlation between temporal paleo-climate variation and trait variation could be slightly artefactual. I admit that a mechanism for this is not obvious. For example it would require that the 100x100km cells that had high temporal climate variability also had high contemporary abiotic variation giving rise to higher functional diversity. Even if this were not the case then separate test of individual traits ought to show that traits more strongly related to climate showed a stronger paleo-climate signal and vice versa. I am not suggesting the authors revise their analysis but a greater level of comment would be useful. The authors openly allude to some of these difficulties at bottom of page 29 but I think a deeper consideration is needed.

We appreciate this point, which was also raised (in the context of megafauna drivers of traits) by another reviewer. In response we have extensively revised and extended the page the reviewer mentions. We now highlight the importance of soil as a possible driver of traits, and also the indirect role of megafauna. However we note that in both cases, we do not yet have the time-series data available to determine the role of these variables relative to climate. We are also optimistic that such analyses will become possible in the near future.

Refs:

Ordoñez, JC et al (2009) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global.Ecol.Biogeogr.* 18, 137-149.

Wright, IJ et al (2005) Modulation of leaf economic traits and trait relationships by climate. *Global.Ecol.Biogeogr.* 14, 411-421.