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## Functionally distinct tree species support long-term productivity in extreme environments

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### Abstract :

Despite evidence of a positive effect of functional diversity on ecosystem productivity, the importance of functionally distinct species (i.e. species that display an original combination of traits) is poorly understood. To investigate how distinct species affect ecosystem productivity, we used a forest-gap model to simulate realistic temperate forest successions along an environmental gradient and measured ecosystem productivity at the end of the successional trajectories. We performed 10 560 simulations with different sets and numbers of species, bearing either distinct or indistinct functional traits, and compared them to random assemblages, to mimic the consequences of a regional loss of species. Long-term ecosystem productivity dropped when distinct species were lost first from the regional pool of species, under the harshest environmental conditions. On the contrary, productivity was more dependent on ordinary species in milder environments. Our findings show that species functional distinctiveness, integrating multiple trait dimensions, can capture species-specific effects on ecosystem productivity. In a context of an environmentally changing world, they highlight the need to investigate the role of distinct species in sustaining ecosystem processes, particularly in extreme environmental conditions.

**Keywords :** functional rarity, functional distinctiveness, biodiversity and ecosystem functioning, productivity, virtual ecology, forest-gap model

## 50 Introduction

51 Two decades of research have shown that ecosystem processes - such as productivity,  
52 nutrient cycling, or temporal stability - depend on emergent properties of ecological  
53 communities, species number and functional diversity in particular [1–3]. This focus on  
54 community-aggregated properties tends to view the roles of individual species as idiosyncratic  
55 [4], or, when particular species are considered, the focus is put on dominant species only [5,6],  
56 which are seen as optimal phenotypes in a given environment [7]. As a consequence, there has  
57 been a blind spot regarding the contribution of species that have an original combination of  
58 functional traits, namely *functionally distinct species* [8].

59 Recent studies suggest that functionally distinct species can play important roles in the  
60 functioning of ecosystems, mediated by various mechanisms. First, they are likely to sustain  
61 functions that are not performed by other species [9], thus increasing the whole ecosystem  
62 functionality through complementarity mechanisms [1,10]. Second, they can increase the  
63 resistance of communities in response to environmental change by being adapted to a broader  
64 range of environmental conditions [8]. Third, they can contribute to lowering community-wide  
65 competition through greater trait dispersion [11]. However, empirical evidence supporting the  
66 importance of distinct species in regulating ecosystem functioning remains scarce [12,13] and  
67 the lack of experimental manipulation of the number and identity of functionally distinct  
68 species impedes a thorough exploration of their role in driving ecosystem dynamics and  
69 functioning.

70 The effects of biodiversity on ecosystem functioning depend on environmental  
71 conditions such as climate or soil [14–16], which have both direct impacts on plant physiology  
72 and indirect influence on community composition [17,18]. Changes in assembly rules and  
73 community composition along environmental gradients can impact ecosystem properties in  
74 various ways, including by affecting species interactions [19], or by modifying the identity of  
75 dominant species (“mass-ratio effect” [5,6,20]), which could be either functionally ordinary or  
76 distinct depending on the environment [8,21]. Whether and how much environmental  
77 conditions modulate the effects of distinct species on ecosystem productivity remains  
78 unexplored, partly because experiments manipulating the composition of communities on  
79 gradients at large scales can be difficult to perform. One way of overcoming this problem is to  
80 use simulation experiments [22], which can be performed over large spatial and temporal  
81 scales, and at the same time manipulate various parameters of interest.

82 Here, we used ForCEEPS (Forest Community Ecology and Ecosystem Processes  
83 [23,24]), a process-based forest succession model that explicitly involves ecological processes,  
84 mainly succession in small patches (up to 1000 m<sup>2</sup>) and competition for light between trees.  
85 This model has several features that make it a useful simulation tool to test the effects of  
86 functionally distinct species on ecosystem functioning. First, the species in the model have  
87 functional trade-offs (e.g., between growth and tolerance to competition) calibrated to existing  
88 tree species [24–26], making it a realistic tool to compute distinctiveness in a multidimensional  
89 trait space. Second, this model has originally been developed to study successions  
90 independently from ecosystem functioning, and thus ecosystem properties are emergent  
91 properties that arise from the modeled forest dynamics and are not directly controlled in the  
92 simulations. ForCEEPS has successfully been applied to study biodiversity-ecosystem  
93 functioning theory [26,27], and to implement biodiversity loss experiments [28]. Third, its  
94 calibration and validation rely on predictions of both annual productivity, which reflects  
95 ecosystem energy and matter dynamics and is one of the most commonly measured ecosystem  
96 processes, and community composition including species relative abundance in the long term  
97 [24]. Fourth, it has been calibrated for a wide range of environmental conditions [24,29], which  
98 provides an excellent opportunity to investigate how the effects of distinct species will change  
99 along environmental gradients.

100 We used the ForCEEPS forest-gap model [24] to simulate communities undergoing  
101 2,000 years of succession from bare ground along an environmental gradient, and to measure  
102 ecosystem annual productivity at equilibrium. We initiated independent successions with  
103 varying species richness - from 30 to 1 tree species - to mimic the consequences of regional  
104 species loss. At each regional richness, we compared ecosystem productivity, measured in three  
105 scenarios (including only the most distinct species, the least distinct species, or random  
106 assemblages), to test the following predictions:

- 107 (1) The loss of functionally distinct species reduces ecosystem functioning in the long  
108 term. We expect ecosystem productivity to decrease faster when distinct species  
109 are lost from the regional pool first than in any other configuration (Fig. 1).
- 110 (2) Environmental conditions modulate the effects of distinct species on ecosystem  
111 functioning. If so, support for prediction (1) depends on the environmental  
112 conditions across the 11 sites.

113

## 114        Methods

### 115        Forest succession model

116            We used the ForCEEPS forest gap model (Forest Community Ecology and Ecosystem  
117    ProcessS, [http://capsis.cirad.fr/capsis/help\\_en/forceeps](http://capsis.cirad.fr/capsis/help_en/forceeps) [24], which was developed on the  
118    Capsis modelling platform [30]. A forest gap model simulates forest successions in small,  
119    independent patches of forest, by explicitly modeling the establishment, growth, and mortality  
120    of tree individuals. This model relies on the same basic assumptions as the historical FORCLIM  
121    (Forest-Climate) model [31,32]. First, the establishment and growth of individuals depend on  
122    the environment: bioclimatic conditions (temperature and water availability), soil nutrient  
123    content, and browsing intensity [24]. Second, they are affected by biotic interactions that are  
124    implemented through competition for light. Finally, individual tree mortality is stochastic, with  
125    an increasing probability with age. A thorough description of the model is provided in appendix  
126    1, and more details on the model calibration and equations can be found in [23,24,26].

127

### 128        Species pool and species traits

129            We considered 30 forest tree species occurring in European mountains, whose  
130    behaviour is simulated by the model. The parameters describing species properties were  
131    calibrated on traits from forest inventories and from measures available from the literature, and  
132    take into account critical trade-offs in species biology (e.g. growth in full light/survival under  
133    shade) [24].

134            A set of 14 parameters was used to characterize each species (the meaning and values  
135    of parameters are given in Table S1). Response-to-driver parameters mechanistically drive  
136    species establishment and survival (through response to water and nitrogen availability,  
137    browsing tolerance, temperature requirements), and intrinsic parameters determine species  
138    growth, competition for light, and succession dynamics (see Table S1). The congruence of  
139    these parameters with classical functional traits extracted from the literature was assessed in a  
140    previous study [24]. Because they are involved in mechanisms that functional traits  
141    approximate, and because they correlate with usual functional traits, these 14 parameters will  
142    be referred to as “traits” hereafter.

143

## 144 Functional distinctiveness computation

145 We ranked species according to their functional distinctiveness computed within the  
146 30-species-rich regional pool of species. Functional distinctiveness is a measure of species  
147 originality in a multidimensional trait space, which can be performed irrespective of species  
148 abundance [33] (cf. Fig. 1A). To avoid over-emphasizing a particular set of correlated traits  
149 (Fig. S1), we first performed a Principal Component Analysis on the fourteen traits and retained  
150 the first four axes that explained 72.2% of the total variance (Fig. 3A, Fig. S2). We then  
151 computed Euclidean distances between species using their scores on these axes with the  
152 `compute_dist_matrix()` function from the `funrar` package v.1.4.0 [33]. We used these  
153 distances to compute each species' functional distinctiveness, which is the average functional  
154 distance of a given species to all the other species, using the `distinctiveness_com()`  
155 function from the same package. We finally ranked species according to their distinctiveness  
156 value.

157 We investigated the sensitivity of this ranking to the traits used through a bootstrap  
158 procedure. We did so by subsampling species trait values with replacement, recomputing the  
159 functional distinctiveness index for all species with the same procedure, and correlating the  
160 new ranking of the species with the one computed on the 14 traits, using Spearman's rank  
161 correlation coefficient (Fig. 3B). The procedure was repeated 10,000 times.

162

## 163 Environmental gradient

164 Relying on the ForClim model [26,32], from which ForCEEPS has been derived, the  
165 model was parameterized for 11 sites in Switzerland and Germany, distributed along a broad  
166 gradient of temperature and water availability (Fig. 4A). Each site was defined by its  
167 geographic position (latitude, longitude, elevation), temperature, and annual precipitation, and  
168 was divided into 50 patches of 800 m<sup>2</sup> each (4 ha per site in total). For each site, 2,000-year-  
169 long fluctuations of climatic parameters were implemented based on historical records [25],  
170 providing climate data with inter-annual variability but with no general trend across the 2,000  
171 years (i.e. no climate change effect).

172

## 173 Effects of species distinctiveness on ecosystem productivity

174 Across the environmental gradient, we generated scenarios in which the regional pool,  
175 composed of 30 European tree species, lost sequentially one species, then two, three, etc. These  
176 scenarios correspond to richness gradients (from 30 to one species), in which the most distinct

177 or the most ordinary species were lost between each richness level of the gradient (Fig. 2). In  
178 each site, and for each richness gradient, we thus simulated 30 independent forest communities  
179 (one at each richness level), undergoing 2,000 years of succession starting from bare ground,  
180 and measured ecosystem productivity in the last 1,000 years (Fig 2. A,B). For the sake of  
181 clarity, the richness gradient scenario in which species were ranked from the most distinct to  
182 the most ordinary will be referred to as “distinct species lost first” (and conversely, the other  
183 scenario will be referred to as “ordinary species lost first”, cf. Fig. 2C). To compare the results  
184 to random expectations, we generated 30 random species richness gradients, and implemented  
185 the same procedure, i.e. for each of the 30 random rankings, species were sequentially lost from  
186 the regional pool, and we simulated a community undergoing succession at each richness level.  
187 A total of 10,560 simulations were run for the 11 sites.

188         Since we started all simulations from bare ground, we measured ecosystem productivity  
189 after the community reached a pseudo-equilibrium for biomass and species composition (from  
190 year 1,000 on), to avoid any effects due to transient dynamics [25] (Fig. S3). After this 1,000-  
191 year-long transient period, mean productivity was computed by averaging the productivity  
192 (accumulated biomass during a year) of ten years sampled every 100 years (i.e. at year 1,100,  
193 1,200,... 2,000), to minimize temporal autocorrelation [26,27]. A confidence interval of the  
194 productivity of the community at each species richness level was computed on the 30 random  
195 removal rankings. Since data were not normally-distributed, we used a non-parametric  
196 approach to build a confidence interval of the median at each species richness level. This  
197 interval is not biased by the sample size: it covers the true median of a population using a  
198 subsample that depends on the population size (30 here), and on the confidence chosen (95%  
199 here) [26,34].

200         To summarize the effects of distinct and ordinary species in each site, we computed the  
201 area under the red curves, or AUC (Fig. 4B) for scenario 1 (“distinct species lost first”) and  
202 under the blue curves for scenario 2 (“ordinary species lost first”). To allow inter-site  
203 comparison, we then divided this AUC by the productivity of the site computed when all the  
204 30 species were present in the regional pool. We finally plotted the resulting relative area under  
205 the curve against site mean annual temperature to compare the sites.

206         Finally, to study the behavior of species in the absence of interspecific interactions, we  
207 measured the biomass and productivity of each species in monoculture. We then tested  
208 potential links between species biomass and productivity in monoculture in each site and their  
209 distinctiveness using Spearman’s rank correlation coefficient.

210         All analyses were performed using R version 4.0.3 [35].

212 

## Results

213 The first two PCA axes represented 52% of total trait variance, and were used to map  
214 the position of the 30 species in trait space (Fig. 3A). On the first axis, strategies ranged from  
215 shade-intolerant species (high values of shade-sensitivity traits Ly and La - see Fig. 3 for  
216 descriptions of traits) that were adapted to cold (low annual required degree-day sum DDMin;  
217 e.g., *Pinus montana*, *Alnus viridis*, Fig. 3A), to shade-tolerant, cold-sensitive, nutrient-  
218 demanding species (e.g., *Ulmus glabra*, *Tilia platyphyllos*). On the second axis, positive values  
219 corresponded to species with long life-span and tall stature (high maximum age AMax and  
220 height HMax), tolerant to drought (DrTol trait), but sensitive to herbivory at a juvenile stage  
221 (Browsing trait; e.g. *Abies alba*, *Taxus baccata*). Species with negative values on the 2nd axis  
222 included those sensitive to drought but not susceptible to herbivory (e.g. *Populus nigra*, *Salix*  
223 *alba*), and with a high growth speed (trait G), but a low maximum age and height (AMax and  
224 HMax). Many functionally ordinary species showed, as expected, intermediate values for most  
225 of the traits (e.g., *Sorbus aria*, *Acer campestre*). A portion of ordinary species was located  
226 towards positive values on the first dimension (e.g. *Acer platanoides*, *Ulmus glabra*), and the  
227 others towards negative values on the second dimension (e.g. *Populus nigra*, *Salix alba*). On  
228 the contrary, the 30% most distinct species were located in three peripheral zones of the trait  
229 space (Fig. 3A, grey circles). Species distinctiveness ranking computed after bootstrapping the  
230 traits correlated with that computed on all the traits, with an average Spearman's rho of 0.739  
231 (Fig. 3B). Rho followed an unimodal distribution centered on rho = 0.747, with a standard  
232 deviation of 0.096.

233 Ecosystem productivity generally decreased with the number of species lost and varied  
234 with the environment (Fig. 4). Warm and wet sites (e.g., Adelboden, Huttwil) had the highest  
235 productivities, with values up to 3t/ha, whereas it did not exceed 1.5 to 2 t/ha in the cold sites  
236 (e.g. Grande Dixence), or warm and dry sites (e.g. Sion). When species were removed in  
237 random order (grey surface, Fig. 4), the productivity of the ecosystem either decreased steeply  
238 (in warm-wet sites, e.g. at Adelboden or Bern), or first remained constant and then decreased  
239 (e.g. in cold sites such as Bever or Cottbus). The effects of distinctiveness-driven species  
240 removal on ecosystem productivity varied across the environmental gradient. In the three  
241 coldest sites (Grande Dixence, Bever, and Davos), productivity decreased more rapidly when  
242 distinct species were lost first (red curves, Fig. 4), than when species loss was random (grey  
243 surface) or when ordinary species were lost first (blue line). This was also the case for one



244 warm-dry site, Sion. On the contrary, in three warm-wet sites (Adelboden, Huttwil, Bern),  
245 productivity decreased more rapidly when ordinary species were lost first (blue curves, Fig. 4).  
246 This trend was also apparent, but less significant, in warm sites with intermediate levels of  
247 rainfall (Schaffhausen, Basel). Finally, in the two remaining sites (Schwerin and Cottbus), there  
248 was no significant difference in productivity between species richness gradients. These results  
249 are summed up in Fig. 5: when distinct species were lost first, the cumulative productivity at  
250 all richness levels (standardized by site productivity) was indeed lower in the extreme sites  
251 (sites 1, 2, 3, and 11, Fig. 5A) than in the other sites. When ordinary species were lost first, on  
252 the contrary, cumulative productivity was slightly higher in these harsh sites than in other sites.  
253 Productivity was thus dependent on the presence of functionally distinct species in harsh (either  
254 cold or warm and dry) environments, whereas it depended more on ordinary species in milder  
255 conditions.

256

257 Trends of decreasing productivity with biodiversity erosion were not monotonous. In  
258 some cases, the loss of one single species led to a strong decrease in ecosystem productivity -  
259 for instance when the 5<sup>th</sup> and 6<sup>th</sup> species (*Pinus cembra* and *Larix decidua*) were removed from  
260 the coldest site (Grande Dixence), the productivity dropped from about 1.2 t.ha<sup>-1</sup>.year<sup>-1</sup> to  
261 almost 0.6 ( Fig. 4 and see table S1 for species distinctiveness ranking). In other cases, species  
262 removal led to an increase in ecosystem productivity, indicating the suppression of a negative  
263 interspecific interaction (e.g., when the 9<sup>th</sup> most distinct species, *Picea abies*, was lost from the  
264 wettest site, Adelboden, productivity increased from about 2.4 to 3 t.ha<sup>-1</sup>.year<sup>-1</sup>, Fig. 4, table  
265 S1). To study the behavior of species across the environmental gradient in the absence of these  
266 interspecific interactions, we measured the productivity of each species grown in monoculture  
267 in each site. The number of species persisting in monoculture was smaller in the cold and warm-  
268 dry environments than in milder conditions (Fig. S4), indicating a stronger abiotic filtering in  
269 harsh environmental conditions. Species that persisted in these sites belonged mostly to the  
270 30% most distinct species. In addition, the correlation between species productivity in  
271 monoculture and their distinctiveness was significantly positive in the three coldest sites  
272 (Bever, Grande Dixence, and Davos - table 1). In all the other sites, there was no correlation  
273 between species functional distinctiveness and either biomass or productivity.

274

275

## Discussion

276 Although rarity is a long-studied attribute of species, the rarity of functions has received  
277 little attention [36] until recently [8], and no test of the effects of functionally distinct species  
278 on ecosystem properties has been performed so far. Our simulations of temperate forest  
279 ecosystems dynamics aimed at investigating distinct species' effects on ecosystem productivity  
280 along an environmental gradient. The loss of functionally distinct species from the regional  
281 pool strongly reduced ecosystem-level productivity in sites at the extremes of the  
282 environmental conditions.

283 The reasons for the strong effects of distinct species loss on ecosystem productivity in  
284 harsh (cold and warm-dry) environmental conditions could be that (i) they dominated the  
285 community by being the most abundant and productive species in such conditions [20], (ii)  
286 they provided a larger breadth of options to maintain productivity under annually fluctuating  
287 conditions [8], or (iii) they could maintain ecosystem productivity through interspecific  
288 interactions (i.e. via niche complementarity and/or facilitation) [37–39]. The latter, especially  
289 niche complementarity, could be expected since complex interspecific interactions have been  
290 shown to be central to the forest ecosystem dynamics simulated by ForCEEPS [26], and  
291 resulted in non-linear, non-monotonous decrease of ecosystem productivity along the species  
292 richness gradient. When simulating monoculture experiments along the environmental  
293 gradient, we showed that distinct species remained the most productive in cold sites: their  
294 overall effect on ecosystem productivity could still be seen without biotic interactions. In cold  
295 sites, distinct species were the most abundant and productive of the community because of their  
296 response to the abiotic environment. On the contrary, at the other extreme of the environmental  
297 gradient (i.e. in warm-dry sites), although distinct species sustained productivity too, they were  
298 neither more abundant nor more productive than ordinary ones. We further performed a  
299 partitioning analysis of biodiversity effects (Appendix 3) which tends to show that distinct  
300 species might have sustained productivity in warm-dry sites through complementarity with the  
301 other species, and not by being the dominant ones in such environments. Even if the relatively  
302 low number of sites along our environmental gradient does not allow for generalization, this  
303 result opens an interesting direction for future research. Species distinctiveness, measured on  
304 a multidimensional trait space involving traits linked to species, species growth, size and age,  
305 their ability to compete for light and tolerate shade, and their response to the abiotic  
306 environment, thus emerged as an integrated index indicating the ability of species to sustain

307 ecosystem productivity in environments at the extremes of the gradient, although the  
308 mechanisms involved might vary depending on the environment.

309 Interestingly, our analysis revealed that, in the coldest sites, the system experienced sudden  
310 drops in productivity when few of the most distinct species went extinct. Few species were  
311 indeed both cold-adapted and productive, leading to low functional redundancy in the  
312 community. As functional redundancy can act as an insurance against the consequences of  
313 species losses [40–42], the loss of the few species displaying the adequate traits was not  
314 compensated for by the remaining species, which was sufficient to trigger abrupt changes and  
315 lose most of the productivity of the ecosystem. Even though functional redundancy is often  
316 measured on effect traits [42,43], and contrary to the tendency of biodiversity and ecosystem  
317 functioning studies to put the emphasis on grouping species according to their functional effect  
318 traits [44,45], our results also evidenced the primary importance of species response to the  
319 abiotic environment. Likely explanations for this bias of emphasize on effect traits can be that  
320 (1) measures in field experiments are made on plants that have already passed the abiotic filter,  
321 in which case effect traits are a more relevant grouping criteria than response traits, or (2)  
322 manipulative experiments are often made in homogeneous abiotic environments, which  
323 explains the emphasis put on effect traits (but see [46]). Prior to considering effect traits,  
324 assessing the diversity of response to the abiotic environment appears as a necessary step [43].  
325 The importance of environmental gradients and their interactions with species response traits  
326 in studying the effects of biodiversity on ecosystems cannot be overstated. Yet, since response  
327 and effect traits are difficult to disentangle in practice [47], how much the response of particular  
328 (here, functionally distinct) species can drive ecosystem properties can be fruitfully  
329 investigated along environmental gradients, as shown in this study.

330 The measure of distinctiveness is, by construction, relative to the traits included in the  
331 calculation [8,40]. Interestingly, distinctiveness rankings computed after bootstraps  
332 significantly correlated with the distinctiveness ranking computed on all the traits. The scores  
333 on the main PCA axes used to compute distinctiveness were thus robust to bootstrapping  
334 because several traits contributed to each of the main axes, indicating that distinctiveness  
335 informed on phenotypes integrated in a multi-trait space. When using traits from the TRY  
336 database [48] the distinctiveness ranking computed on traits linked to growth and leaf  
337 economics strategy (Specific Leaf Area, nitrogen content and plant height) correlated with the  
338 ranking computed on the 14 parameters of the model used as traits, giving confidence in the

339 robustness of this metrics (see supplementary analysis). Yet, the correlation was not significant  
340 when distinctiveness was computed on the six traits used by Diaz et al. [49] (Appendix 4, Fig.  
341 S6). This is not surprising, since these six traits were chosen by the authors to maximize the  
342 dispersion of species in a multivariate analysis, and are thus likely not to reflect with accuracy  
343 the ecological processes, such as growth or competition for light, that are modelled in  
344 ForCEEPS. More broadly, our results should, of course, be taken with care, since the present  
345 study relies on simulations from a model, which cannot consider all the processes operating in  
346 nature. First, many mechanisms not included in the model could mediate an effect of distinct  
347 species on ecosystem properties. For instance, in addition to complementarity in the access to  
348 light, distinct species can be involved in other mechanisms, e.g. plant-soil feedbacks, which  
349 are not included in the model, but which may have an effect on ecosystem processes such as  
350 nutrient cycling [16,50] (e.g. nitrogen-fixing plants should be distinct, and should affect  
351 nitrogen cycle more than other species via their interactions with soil bacteria). Second, the  
352 distinctiveness index was computed at a regional scale, with a limited set of species  
353 implemented in the model (e.g. many shrubs are absent from ForCEEPS). Although this  
354 enabled us to evidence that functionally distinct species were driving ecosystem productivity  
355 in the extremes of a regional climatic gradient, and that this effect was independent from biotic  
356 interactions in cold sites (where the effect was the strongest), computing distinctiveness at a  
357 local scale (which should be done only when realized species richness is high enough for this  
358 index to be meaningful, cf. Fig. S4) may be a way to explore potential roles of distinct species  
359 mediated by complementarity in resource use [1,10], or by a reduction of competition through  
360 trait dispersion [11]. At a local scale (i.e. that of realized community), distinctiveness ranking  
361 might or might not be correlated to that computed at the regional scale, depending on the  
362 number of species persisting and the functional diversity of the realized community [51].  
363 Overall, depending on the question and the mechanisms implemented in the models, simulation  
364 experiments can be powerful tools to generate predictions and hypotheses based on a  
365 mechanistic examination of ecological systems [22,52], and can pave the way for subsequent  
366 hypothesis-driven empirical tests.

367

## 368 Conclusion

369 Relying on a forest-gap model, we found that functional distinctiveness, a measure of the  
370 originality of a phenotype, can be linked to its role in ecosystem functioning. In particular, at  
371 the regional scale, we showed that functionally distinct species' response to the abiotic

372 environment enabled them to sustain ecosystem productivity in harsh conditions, whereas  
373 productivity depended more on functionally ordinary species in milder conditions. If distinct  
374 species appear to be vulnerable to extinction, they should be considered in conservation plans  
375 aiming at maintaining ecosystem functioning and services in an environmentally changing  
376 world.

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## 388 Author contributions

389 W.T., C.V., P.G., X.M., and L.D. designed research; L.D., C.V., P.G., and X.M.  
390 performed research and analysed data; L.D. wrote the manuscript and all authors critically  
391 revised the manuscript and gave insights on data analysis; C.V. provided fundings and  
392 coordinated the study. All authors gave final approval for publication and agreed to be held  
393 accountable for the work performed therein. The authors declare no competing interest.

## 394 Supporting information

395 Appendix 1: Description of the ForCEEPS forest gap model.

396 Appendix 2: Figures S1, S2, S3, S4, and table S1.

397 Appendix 3: Mechanisms behind functionally distinct species’ effect on productivity.  
398 Figure S5.

399 Appendix 4: Computation of functional distinctiveness on traits from the TRY database.  
400 Figure S6.

401

402

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## Figures and tables

565

566 Figure 1: *Conceptual framework of the study (adapted from [8]). A species is*  
567 *schematically represented by a leaf. Panel A: six species are located in a two-dimension*  
568 *functional trait space. Ordinary species (blue background) are those located in the centre of*  
569 *the distribution in that space, whereas distinct species (red background) are away from that*  
570 *centre. Panel B: Diagram showing the expected level of ecosystem property (in this study,*  
571 *productivity) as biodiversity declines, in the hypothesis that distinct phenotypes support*  
572 *important functions in the ecosystem. Orders of species loss are: distinct first (A), ordinary*  
573 *first (B), or random (C).*

574

575 Figure 2: *Experimental design. Panel A: a simulation followed three steps. Species*  
576 *were ranked according to their distinctiveness, which is represented by a gradient of colors,*  
577 *from blue (ordinary species) to red (distinct species). Panel B: To implement biodiversity loss*  
578 *scenarios, simulations were made using several pools of species. Each pool on the x axis is a*  
579 *subset of the pool located at its left (which is represented by the sign >). For each pool of*  
580 *species, a simulation was made and the ecosystem productivity was measured and represented*  
581 *on the y axis. Panel C: the process was repeated for three designs. Design 3, in which species*  
582 *were lost randomly, was repeated 30 times to give a null distribution against which the results*  
583 *of designs 1 and 2 could be plotted.*

584

585 Figure 3: *Position of the species in the trait space, and distinctiveness computation.*  
586 *Panel A: Position of the species on the two first axes of a PCA computed on ForCEEPS traits.*  
587 *Species are labelled. Their distinctiveness is coded by a gradient of colour, from blue*  
588 *(functionally ordinary species) to red (functionally distinct species). The 30% most distinct*  
589 *species are evidenced by three grey circles, and the name of strategies describing their trait*  
590 *combinations is given. Panel B: Sensitivity of distinctiveness ranking to the traits used. Traits*  
591 *were bootstrapped 10000 times, and for each bootstrap, the new distinctiveness ranking was*  
592 *correlated with the one computed on all the traits, using Spearman's rank correlation*  
593 *coefficient. The distribution of rho is given (mean = 0.739, median = 0.747, sd = 0.096).*  
594 *Parameters are, in alphabetic order: **Amax**: Maximum age (years); **A1max and A2**: Crown*  
595 *size allometry parameters; **Brown**: Browsing susceptibility of seedlings (from 1, least*

596 *susceptible, to 5, most susceptible); **DDMin**: Minimal required annual degree-days sum (°C);*  
597 ***DrTol**: Drought tolerance index (unitless, continuous from 0, sensitive, to 1, tolerant); **G**:*  
598 *Optimal growth (unitless); **HMax**: Maximum height (m); **La**: Shade tolerance of adults (from*  
599 *0, tolerant, to 1, sensitive); **Ly**: Shade tolerance of seedlings (from 0, tolerant, to 1, sensitive);*  
600 ***NTol**: Soil nitrogen requirements (from 1, weak requirements, to 5, strong requirements); **S**:*  
601 *Allometry between diameter and height (unitless); **WiTN**: Monthly minimum winter*  
602 *temperature tolerated for regeneration (°C); **WiTX**: Monthly maximum winter temperature*  
603 *tolerated for regeneration (°C).*

604

605 *Figure 4: Changes in productivity of the simulated forests caused by species loss in*  
606 *different environmental conditions. Panel A: the 11 sites are numbered and located by dots in*  
607 *a temperature/precipitation graph, and classified into four categories. Panel B: the*  
608 *consequences on ecosystem productivity of the loss of functionally distinct species (red*  
609 *continuous line), ordinary species (blue dashed line), or of random species losses (grey*  
610 *surface), are shown for each site, and the correspondence with site number in panel A is given.*

611

612 *Figure 5: Relative area under the curve (AUC) of each scenario of species loss (distinct*  
613 *species lost first, panel A, or ordinary species lost first, panel B, cf. Fig. 2). For each site, in*  
614 *each of the two scenarios, relative AUC corresponds to the sum of the productivity of all the*  
615 *30 simulations, divided by the productivity of the site when all the 30 species were present in*  
616 *the regional pool, to allow intersite comparison. Sites are numbered from 1 to 11 following*  
617 *Fig. 4.*

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620

Site	Biomass		Productivity	
	Correlation	p.value	Correlation	p.value
GrandeDixence	<b>0.62</b>	<b>&lt;0.01</b>	<b>0.6</b>	<b>&lt;0.01</b>
Bever	<b>0.52</b>	<b>&lt;0.01</b>	<b>0.61</b>	<b>&lt;0.01</b>
Davos	<b>0.49</b>	<b>0.01</b>	<b>0.47</b>	<b>0.01</b>
Adelboden	0.29	0.12	0.13	0.5
Huttwil	0.07	0.71	-0.14	0.47
Bern	0.12	0.52	-0.15	0.42
Schaffhausen	0.01	0.97	-0.15	0.44
Basel	-0.02	0.93	-0.19	0.31
Schwerin	0	0.99	-0.07	0.7
Cottbus	-0.11	0.56	-0.15	0.42
Sion	-0.11	0.55	-0.13	0.51

621 Table 1: *Correlation between species distinctiveness and species biomass and productivity in*  
622 *monoculture for each site. Spearman's rank correlation coefficient, and the p-value of the*  
623 *corresponding test, are given for both biomass and productivity. Significant values are*  
624 *highlighted in bold. Sites are ordered as in Fig. 4.*

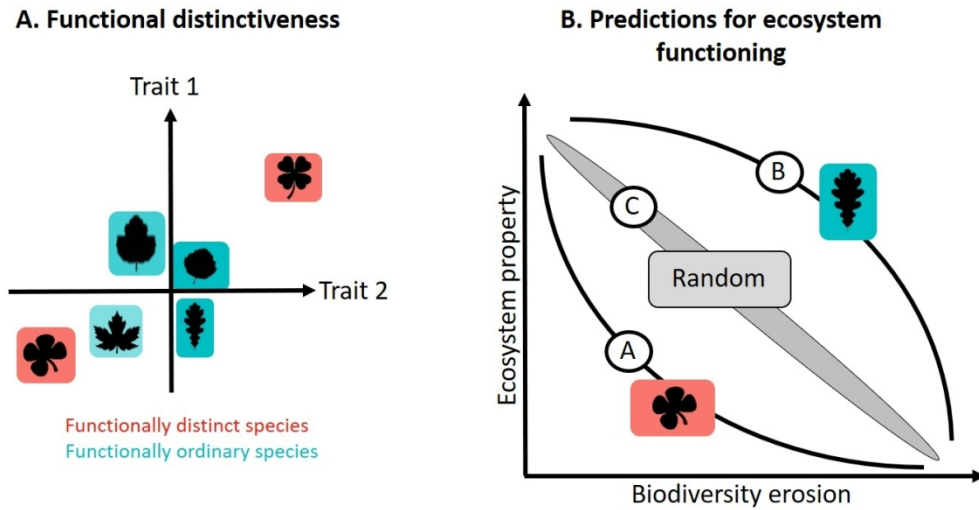


Figure 1: Conceptual framework of the study (adapted from [8]). A species is schematically represented by a leaf. Panel A: six species are located in a two-dimension functional trait space. Ordinary species (blue background) are those located in the centre of the distribution in that space, whereas distinct species (red background) are away from that centre. Panel B: Diagram showing the expected level of ecosystem support property (in this study, productivity) as biodiversity declines, in the hypothesis that distinct phenotypes support important functions in the ecosystem. Orders of species loss are: distinct first (A), ordinary first (B), or random (C).

230x122mm (150 x 150 DPI)

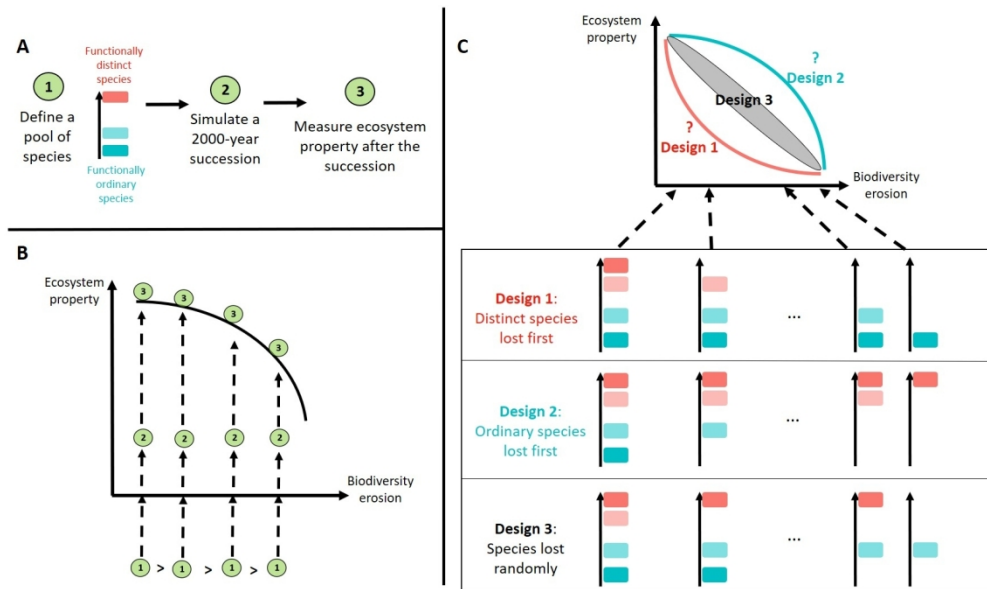


Figure 2: Experimental design. Panel A: a simulation followed three steps. Species were ranked according to their distinctiveness, which is represented by a gradient of colors, from blue (ordinary species) to red (distinct species). Panel B: To implement biodiversity loss scenarios, simulations were made using several pools of species. Each pool on the x axis is a subset of the pool located at its left (which is represented by the sign >). For each pool of species, a simulation was made and the ecosystem productivity was measured and represented on the y axis. Panel C: the process was repeated for three designs. Design 3, in which species were lost randomly, was repeated 30 times to give a null distribution against which the results of designs 1 and 2 could be plotted.

300x176mm (150 x 150 DPI)

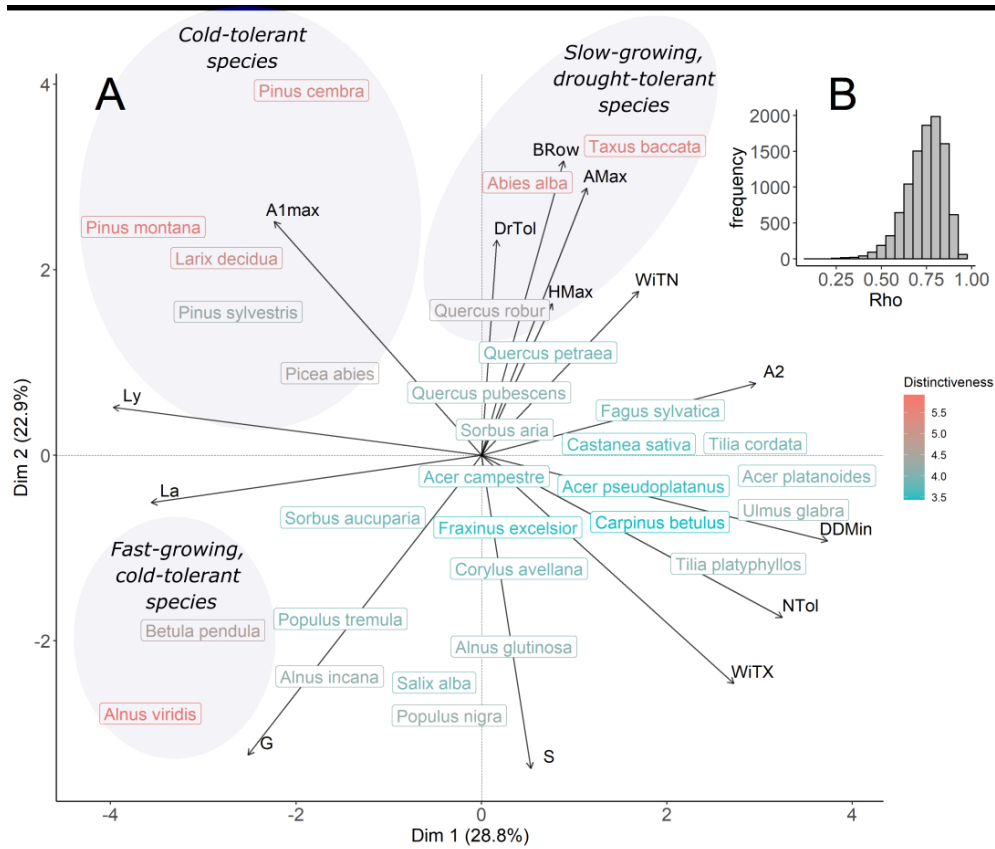


Figure 3: Position of the species in the trait space, and distinctiveness computation. Panel A: Position of the species on the two first axes of a PCA computed on ForCEEPS traits. Species are labelled. Their distinctiveness is coded by a gradient of colour, from blue (functionally ordinary species) to red (functionally distinct species). The 30% most distinct species are evidenced by three grey circles, and the name of strategies describing their trait combinations is given. Panel B: Sensitivity of distinctiveness ranking to the traits used. Traits were bootstrapped 10000 times, and for each bootstrap, the new distinctiveness ranking was correlated with the one computed on all the traits, using Spearman's rank correlation coefficient. The distribution of rho is given (mean = 0.739, median = 0.747, sd = 0.096). Parameters are, in alphabetic order: Amax: Maximum age (years); A1max and A2: Crown size allometry parameters; Brown: Browsing susceptibility of seedlings (from 1, least susceptible, to 5, most susceptible); DDMin: Minimal required annual degree-days sum ( $^{\circ}\text{C}$ ); DrTol: Drought tolerance index (unitless, continuous from 0, sensitive, to 1, tolerant); G: Optimal growth (unitless); HMax: Maximum height (m); La: Shade tolerance of adults (from 0, tolerant, to 1, sensitive); Ly: Shade tolerance of seedlings (from 0, tolerant, to 1, sensitive); NTol: Soil nitrogen requirements (from 1, weak requirements, to 5, strong requirements); S: Allometry between diameter and height (unitless); WiTN: Monthly minimum winter temperature tolerated for regeneration ( $^{\circ}\text{C}$ ); WiTX: Monthly maximum winter temperature tolerated for regeneration ( $^{\circ}\text{C}$ ).

732x661mm (38 x 38 DPI)



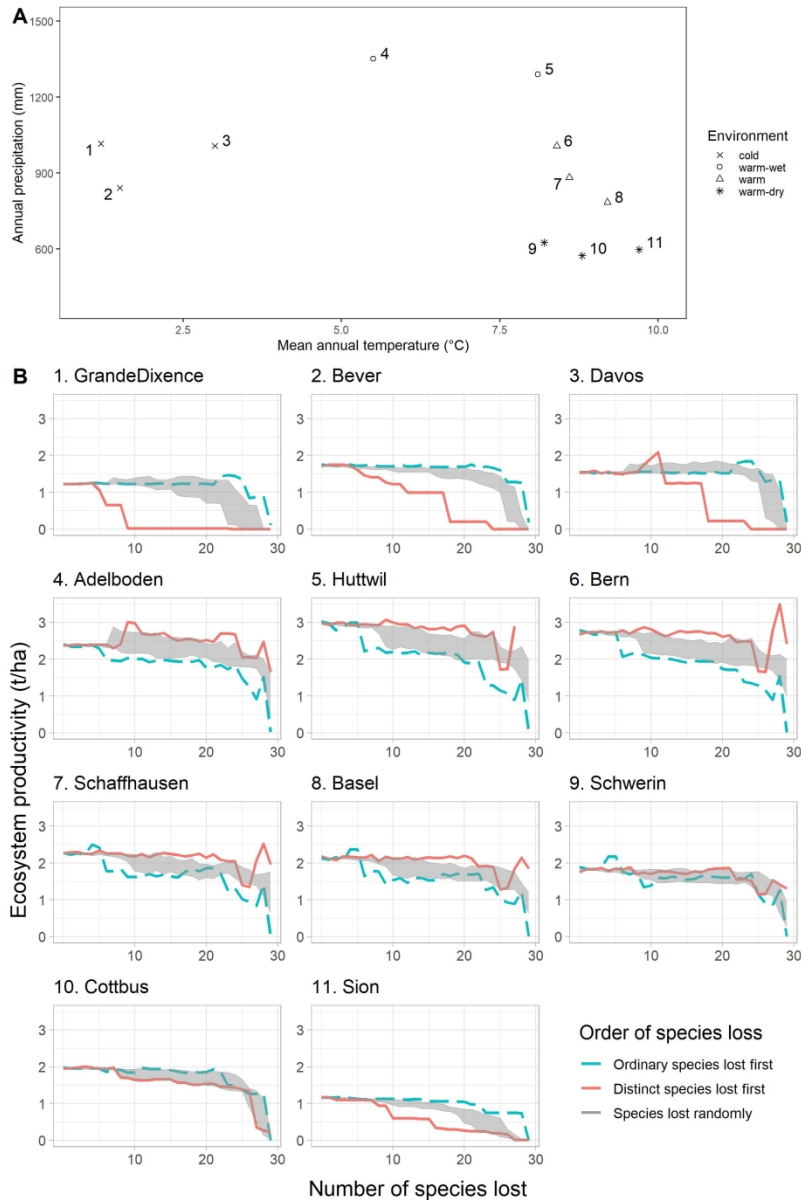


Figure 4: Changes in productivity of the simulated forests caused by species loss in different environmental conditions. Panel A: the 11 sites are numbered and located by dots in a temperature/precipitation graph, and classified into four categories. Panel B: the consequences on ecosystem productivity of the loss of functionally distinct species (red continuous line), ordinary species (blue dashed line), or of random species losses (grey surface), are shown for each site, and the correspondence with site number in panel A is given.

199x299mm (300 x 300 DPI)

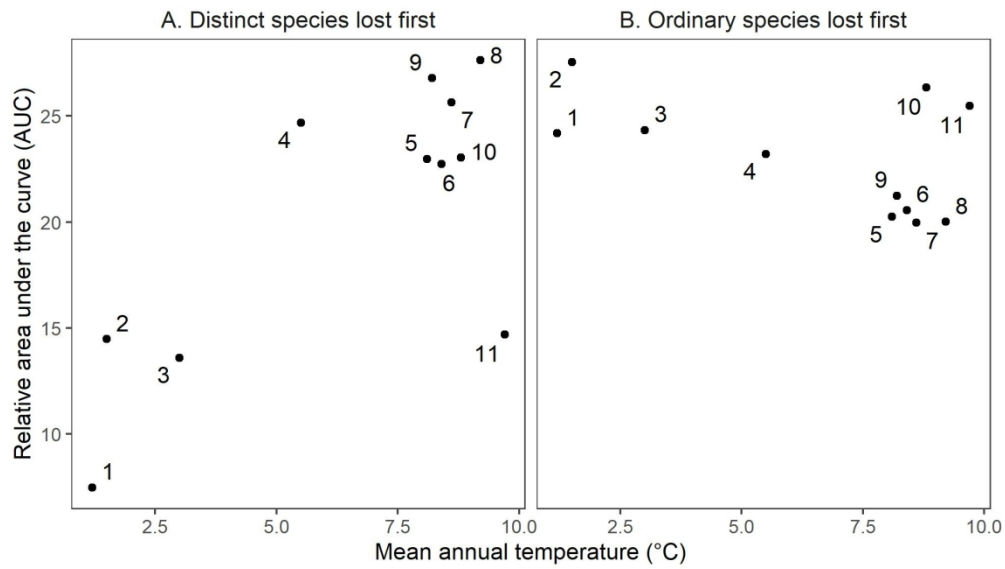


Figure 5: Relative area under the curve (AUC) of each scenario of species loss (distinct species lost first, panel A, or ordinary species lost first, panel B, cf. Fig. 2). For each site, in each of the two scenarios, relative AUC corresponds to the sum of the productivity of all the 30 simulations, divided by the productivity of the site when all the 30 species were present in the regional pool, to allow intersite comparison. Sites are numbered from 1 to 11 following Fig. 4.

169x99mm (300 x 300 DPI)