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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 species impedes a thorough exploration of their role in driving ecosystem dynamics and 68 functioning. 69

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.

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

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 The loss of functionally distinct species reduces ecosystem functioning in the long term. We expect ecosystem productivity to decrease faster when distinct species 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 ProcesseS, 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 1, and more details on the model calibration and equations can be found in [23,24,26]. 126

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#### Species pool and species traits

We considered 30 forest tree species occurring in European mountains, whose behaviour is simulated by the model. The parameters describing species properties were calibrated on traits from forest inventories and from measures available from the literature, and take into account critical trade-offs in species biology (e.g. growth in full light/survival under 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, browsing tolerance, temperature requirements), and intrinsic parameters determine species 137 138 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.

#### 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.

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

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#### 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 was divided into 50 patches of 800 m<sup>2</sup> each (4 ha per site in total). For each site, 2,000-year-168 169 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).

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#### Effects of species distinctiveness on ecosystem productivity

Across the environmental gradient, we generated scenarios in which the regional pool, composed of 30 European tree species, lost sequentially one species, then two, three, etc. These 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 each site, and for each richness gradient, we thus simulated 30 independent forest communities 178 179 (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].

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

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

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

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#### 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.

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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 for instance when the 5<sup>th</sup> and 6<sup>th</sup> species (*Pinus cembra* and *Larix decidua*) were removed from 259 260 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 interspecific interaction (e.g., when the 9th most distinct species, Picea abies, was lost from the 263 wettest site, Adelboden, productivity increased from about 2.4 to 3 t.ha<sup>-1</sup>.year<sup>-1</sup>, Fig. 4, table 264 S1). To study the behavior of species across the environmental gradient in the absence of these 265 266 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.

#### 275 Discussion

Although rarity is a long-studied attribute of species, the rarity of functions has received little attention [36] until recently [8], and no test of the effects of functionally distinct species on ecosystem properties has been performed so far. Our simulations of temperate forest ecosystems dynamics aimed at investigating distinct species' effects on ecosystem productivity along an environmental gradient. The loss of functionally distinct species from the regional pool strongly reduced ecosystem-level productivity in sites at the extremes of the 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 the308 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 hypothesis-driven empirical tests. 366

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#### 368 Conclusion

Relying on a forest-gap model, we found that functional distinctiveness, a measure of the originality of a phenotype, can be linked to its role in ecosystem functioning. In particular, at the regional scale, we showed that functionally distinct species' response to the abiotic environment enabled them to sustain ecosystem productivity in harsh conditions, whereas productivity depended more on functionally ordinary species in milder conditions. If distinct species appear to be vulnerable to extinction, they should be considered in conservation plans aiming at maintaining ecosystem functioning and services in an environmentally changing world.

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#### 388 Author contributions

W.T., C.V., P.G., X.M., and L.D. designed research; L.D., C.V., P.G., and X.M. performed research and analysed data; L.D. wrote the manuscript and all authors critically revised the manuscript and gave insights on data analysis; C.V. provided fundings and coordinated the study. All authors gave final approval for publication and agreed to be held 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.

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.

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#### **Figures and tables**

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).

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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 coefficient. The distribution of rho is given (mean = 0.739, median = 0.747, sd = 0.096). 593 594 Parameters are, in alphabetic order: Amax: Maximum age (years); Almax 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).* 

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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.

611

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.

	Biomass		Productivity	
Site	Correlation	p.value	Correlation	p.value
GrandeDixence	0.62	<0.01	0.6	<0.01
Bever	0.52	<0.01	0.61	<0.01
Davos	0.49	0.01	0.47	0.01
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 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 (°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 (°C); WiTX: Monthly maximum winter temperature tolerated for regeneration (°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)