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.

Introduction

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

Recent studies suggest that functionally distinct species can play important roles in the functioning of ecosystems, mediated by various mechanisms. First, they are likely to sustain functions that are not performed by other species [9], thus increasing the whole ecosystem functionality through complementarity mechanisms [1,10]. Second, they can increase the resistance of communities in response to environmental change by being adapted to a broader range of environmental conditions [8]. Third, they can contribute to lowering community-wide competition through greater trait dispersion [11]. However, empirical evidence supporting the importance of distinct species in regulating ecosystem functioning remains scarce [12,13] and 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 functioning.

The effects of biodiversity on ecosystem functioning depend on environmental conditions such as climate or soil [14–16], which have both direct impacts on plant physiology and indirect influence on community composition [17,18]. Changes in assembly rules and community composition along environmental gradients can impact ecosystem properties in various ways, including by affecting species interactions [19], or by modifying the identity of dominant species ("mass-ratio effect" [5,6,20]), which could be either functionally ordinary or distinct depending on the environment [8,21]. Whether and how much environmental conditions modulate the effects of distinct species on ecosystem productivity remains unexplored, partly because experiments manipulating the composition of communities on gradients at large scales can be difficult to perform. One way of overcoming this problem is to use simulation experiments [22], which can be performed over large spatial and temporal 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 m²) 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

Methods

Forest succession model

We used the ForCEEPS forest gap model (Forest Community Ecology and Ecosystem ProcesseS, http://capsis.cirad.fr/capsis/help_en/forceeps [24], which was developed on the Capsis modelling platform [30]. A forest gap model simulates forest successions in small, independent patches of forest, by explicitly modeling the establishment, growth, and mortality of tree individuals. This model relies on the same basic assumptions as the historical FORCLIM (Forest-Climate) model [31,32]. First, the establishment and growth of individuals depend on the environment: bioclimatic conditions (temperature and water availability), soil nutrient content, and browsing intensity [24]. Second, they are affected by biotic interactions that are implemented through competition for light. Finally, individual tree mortality is stochastic, with 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].

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].

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

Functional distinctiveness computation

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

Environmental gradient

Relying on the ForClim model [26,32], from which ForCEEPS has been derived, the model was parameterized for 11 sites in Switzerland and Germany, distributed along a broad gradient of temperature and water availability (Fig. 4A). Each site was defined by its geographic position (latitude, longitude, elevation), temperature, and annual precipitation, and was divided into 50 patches of 800 m² each (4 ha per site in total). For each site, 2,000-year-long fluctuations of climatic parameters were implemented based on historical records [25], providing climate data with inter-annual variability but with no general trend across the 2,000 years (i.e. no climate change effect).

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

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].

211

Results

212

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 5th and 6th species (*Pinus cembra* and *Larix decidua)* were removed from
260 the coldest site (Grande Dixence), the productivity dropped from about 1.2 t.ha^{-1}.year^{-1} 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 9th most distinct species, *Picea abies,* was lost from the
264 wettest site, Adelboden, productivity increased from about 2.4 to 3 t.ha^{-1}.year^{-1}, 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

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.

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

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

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

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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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.

Supporting information

Appendix 1: Description of the ForCEEPS forest gap model.

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

Appendix 3: Mechanisms behind functionally distinct species' effect on productivity. Figure S5.

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

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562

563

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).*

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	**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*
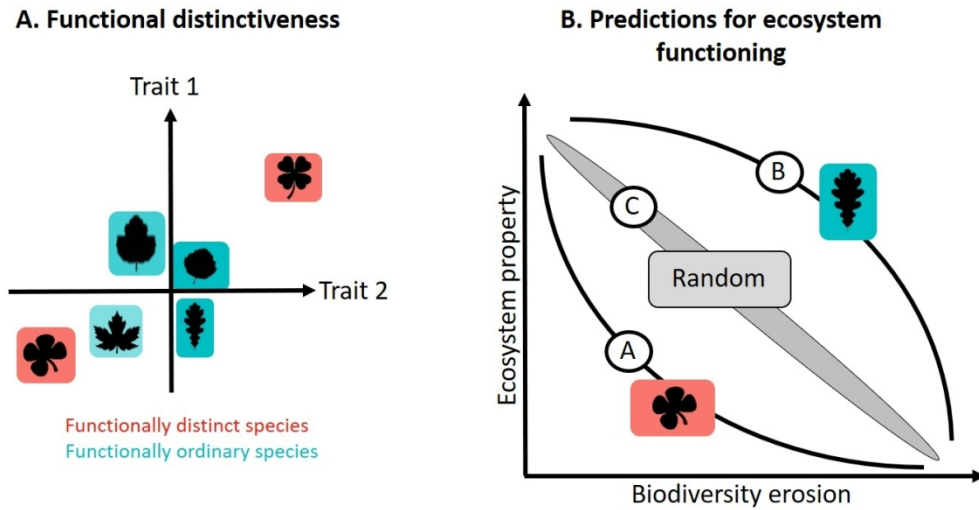624 *highlighted in bold. Sites are ordered as in Fig. 4.*

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).
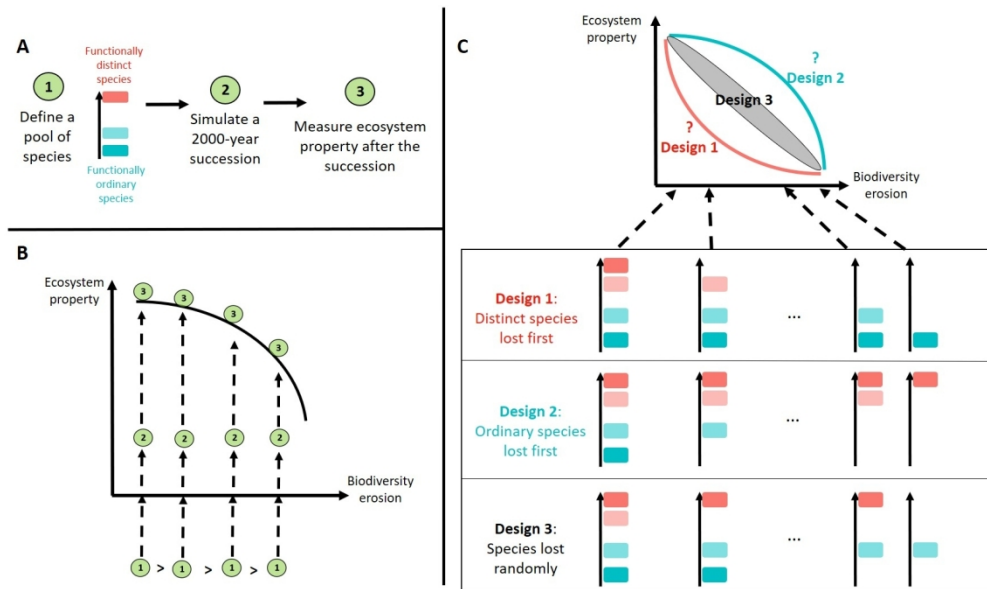
230x122mm (150 x 150 DPI)

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.
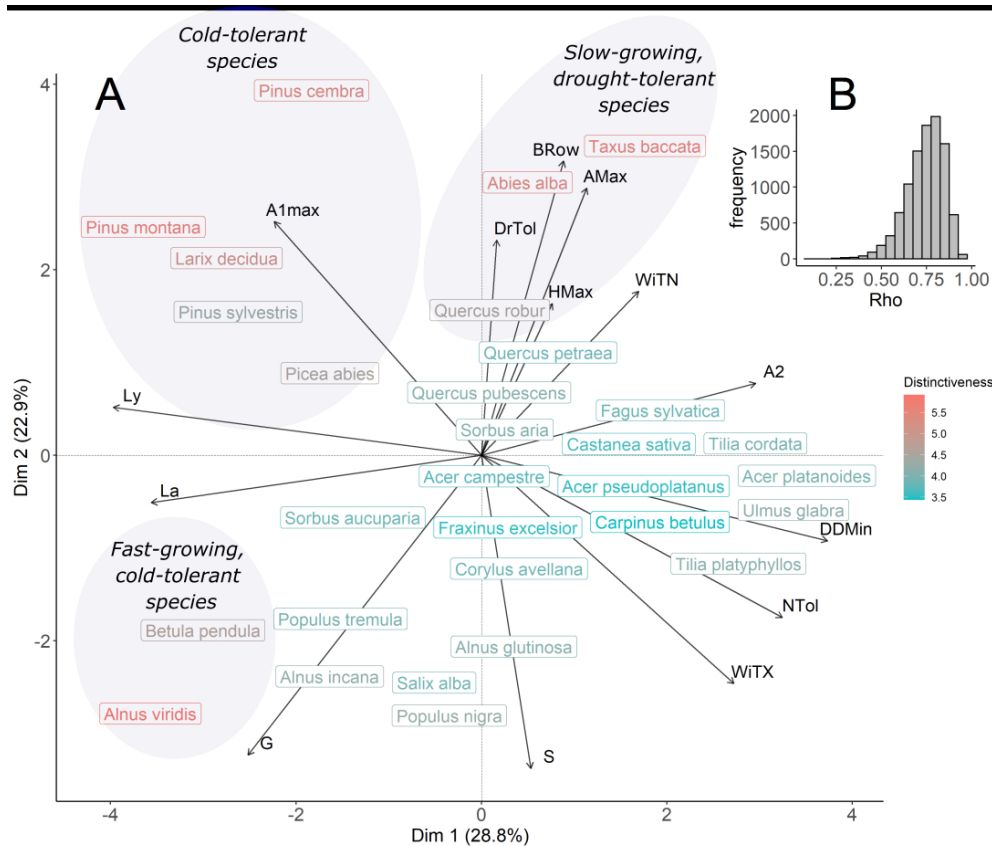
300x176mm (150 x 150 DPI)

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).
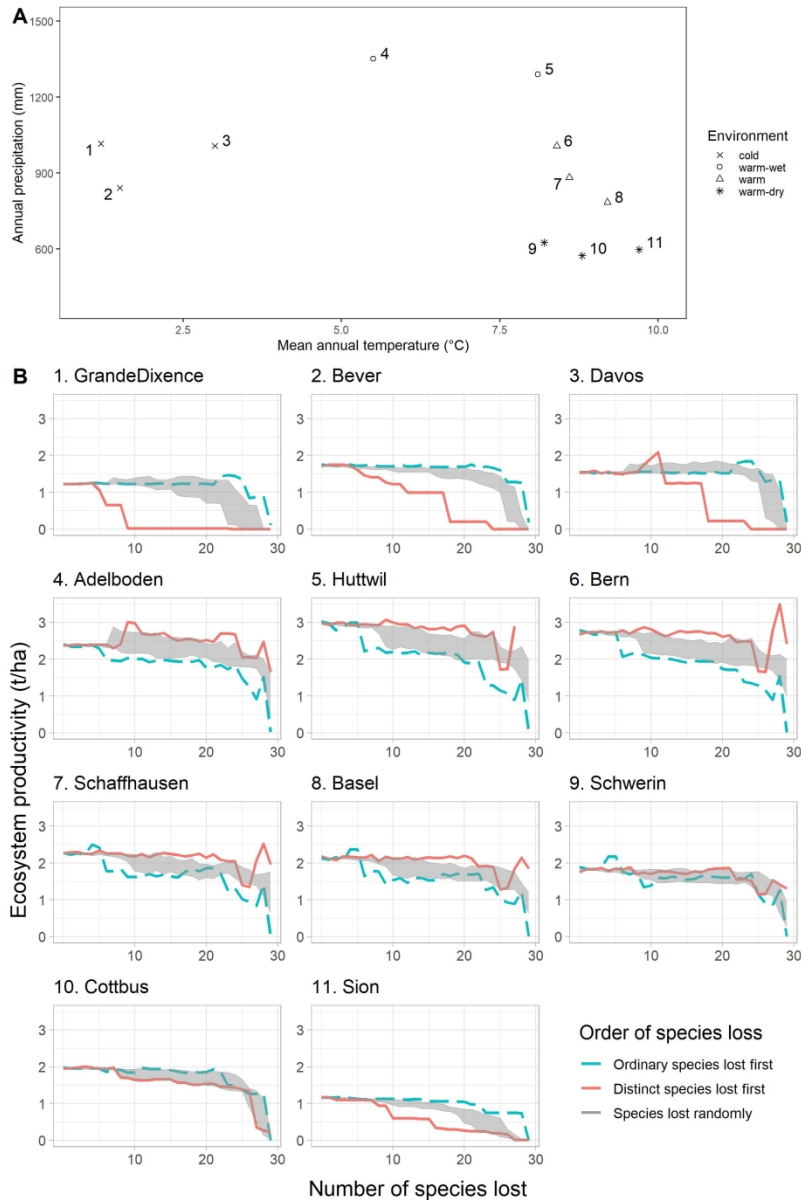
732x661mm (38 x 38 DPI)

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.
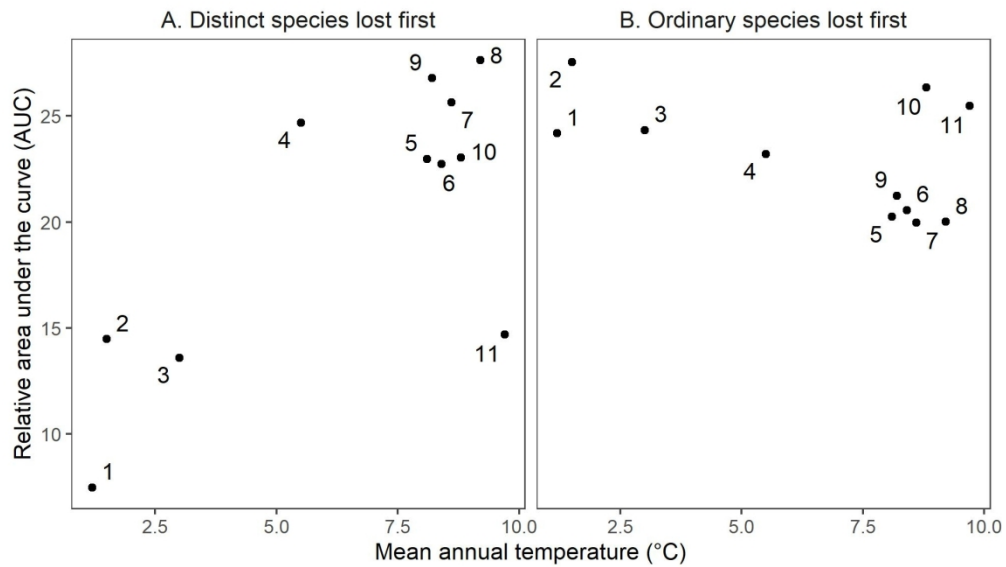
199x299mm (300 x 300 DPI)

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)