

1 **From taxonomic to functional dark diversity: exploring the causes of**
2 **potential biodiversity and its implications for conservation**

3

4 Authors : Loïs Morel¹, Vincent Jung², Simon Chollet², Frédéric Ysnel¹ & Lou Barbe²

5 ¹UMR BOREA, MNHN, CNRS, UPMC, IRD, UC, UA, Université de Rennes 1, Campus Beaulieu,
6 35042, Rennes Cedex, France

7 ²UMR 6553 ECOBIO, OSUR, CNRS, Université de Rennes 1, 35042 Rennes, France

8

9 Corresponding author: Loïs Morel

10 Type of article: **Research article**

11

12 **Authors' contributions**

13 L.M. and F.Y. performed the data collection. L.M. conceived and performed the analyses.

14 L.M and L.B. wrote the manuscript, with the help of V.J., S.C. and F.Y.

15 **Acknowledgements**

16 We are very grateful to the “Région Bretagne”, the “Conseil départemental des Côtes
17 d’Armor”, the “Conseil départemental d’Ille-et-Vilaine” and the “Communauté de
18 communes de Plouha-Lanvollon” which supported financially this work. We also are very
19 grateful to Benoit Dujol for fruitful early discussion about dark diversity.

20 **Data accessibility statement**

21 All the data will be deposit in the Figshare public repository and will be freely available
22 should the paper be accepted.

23

24

25

26 **Abstract**

27 1. Dark diversity is an emerging and promising concept proposed to estimate the recruitment
28 potential of natural communities and guide conservation and restoration policies. It
29 represents all the species that could be present in a community due to favourable
30 environmental conditions, but are currently lacking. To date, experimental approaches only
31 measured taxonomic dark diversity, mainly based on species coexistence, which relies partly
32 on neutral processes. Thus, these approaches may fail to identify the biodiversity which is
33 lacking for deterministic reasons, and can hence hardly bring out suitable restoration
34 methods.

35 2. Here, we propose a novel method to estimate dark diversity, which is based on more
36 deterministic coexistence: the coexistence of species' functional features. We adapted the
37 Beals' co-occurrence index using functional groups, and we estimated functional dark
38 diversity based on coexistence of functional groups. We then made use of functional dark
39 diversity to address a persistent issue of restoration ecology: how does passive rewilding
40 impact the ecological integrity of recovered communities? We compared spontaneous,
41 secondary woodlands with ancient forests, in terms of taxonomic and functional dark
42 diversity of vascular plants and spiders.

43 3. Our results indicated that functional dark diversity does not equate to taxonomic dark
44 diversity. Considering plants, recent woodlands surprisingly harboured less functional dark
45 diversity than ancient forests, while they had a very similar amount of taxonomic dark
46 diversity. Concerning spiders, recent woodlands harboured a similar amount of functional
47 dark diversity as ancient forests, but more taxonomic dark diversity. Also, the composition of
48 functional dark diversity differed between forest types, shedding light on their past assembly
49 processes and unveiling their potential for conservation and effective restoration.

50 4. *Synthesis and applications.* Functional dark diversity brings novel perspectives for ecological
51 diagnostic and restoration. Combined to taxonomic dark diversity, it enables to identify easily
52 the deterministic constraints which limit the re-assembly of ecological communities after
53 land-use changes and to predict the realistic, possible establishments of functional features.
54 Here, we showed that spontaneous woodlands can have very similar, sometimes even
55 higher, ecological integrity than that of ancient forests, and hence may be valuable habitats
56 to be conserved from an ecological perspective.

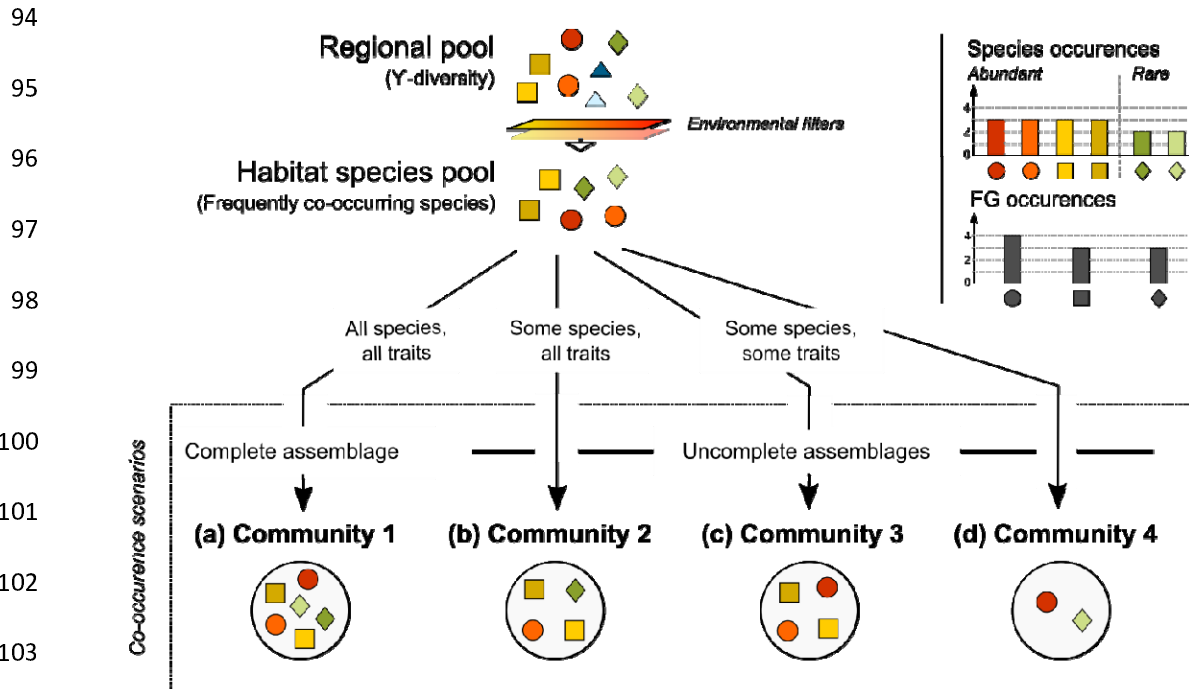
57 **Keywords:** community assembly, ecological restoration, forest temporal continuity, passive
58 rewilding, plants, spiders, taxonomic and functional dark diversity

59 Introduction

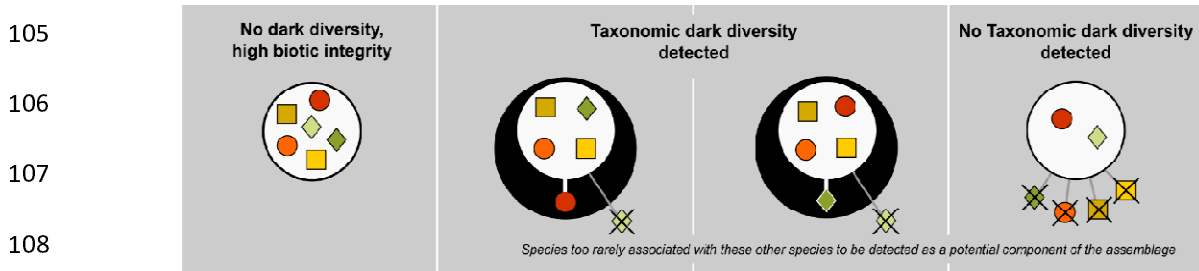
60 The concept of *dark diversity* has recently been introduced in Ecology by Pärtel, Szava-Kovats, &
61 Zobel (2011), to take into account the potential biodiversity of natural communities. In a given
62 community, the dark diversity represents the diversity of species that are locally absent while they
63 are present in the regional pool and could be present due to favourable environmental conditions
64 (*i.e.* they are present in the habitat-specific species pool, Pärtel et al., 2011). Therefore, dark diversity
65 identifies species that are absent due to dispersal limitation or historical contingencies, but not
66 species that are absent due to recruitment limitation (that should be absent anyway) nor species that
67 the sampling failed to observe (dormant or very rare species, see Pärtel, 2014). Dark diversity places
68 biodiversity into a dynamic perspective: for example, it integrates species with a colonisation credit,
69 which are species likely to be recruited in the future due to favourable environmental conditions or
70 delayed population growth (Jackson & Sax, 2010). Moreover, dark diversity sheds light on assembly
71 processes, for example by determining the extent to which stochastic processes such as dispersal
72 influence assembly (Pärtel, 2014; Pärtel et al., 2011). Consequently, identifying the dark diversity of
73 communities enables to guide the conservation efforts and the restoration strategies, since it helps
74 to determine the taxa that are frequently absent (e.g. see Moeslund et al., 2017), the habitats more
75 or less degraded, their restoration potential, and, conversely, the habitats that are the most
76 complete (*i.e.* with the lowest dark diversity, Lewis et al., 2017) and that could hence be priority
77 targets for conservation. However, to date, the studies evaluating dark diversity are restricted to the
78 taxonomic facet of communities, hence to species' identities.

79 Incorporating functional traits of species into direct assessments of dark diversity could bring many
80 novel insights. Functional traits are all the features of species that can either respond to
81 environmental conditions or can impact ecosystem functions, or both (Violle et al., 2007). Basically,
82 these are morphological, physiological or phenological features, for example the life form of a plant
83 or the type of diet of an animal. The tools that are currently available for measuring directly dark
84 diversity do not consider functional traits, overlooking the ecological differences that may exist
85 between or within taxa. Functional traits can obviously be very different among taxa but also within
86 taxa (Prinzing et al., 2008), and in taxa occupying particular environments (Hermant, Hennon,
87 Bartish, Yguel, & Prinzing, 2012). Alternatively, at some trophic level, several species can have similar
88 functional traits and can therefore be redundant in the impact they have on ecosystem functions or
89 in the response they have to disturbances or environmental changes. Consequently, a given
90 taxonomic dark diversity could or could not represent a functional dark diversity (Figure 1b, c, d),
91 which would bring very different information about past assembly processes, the potential outcome

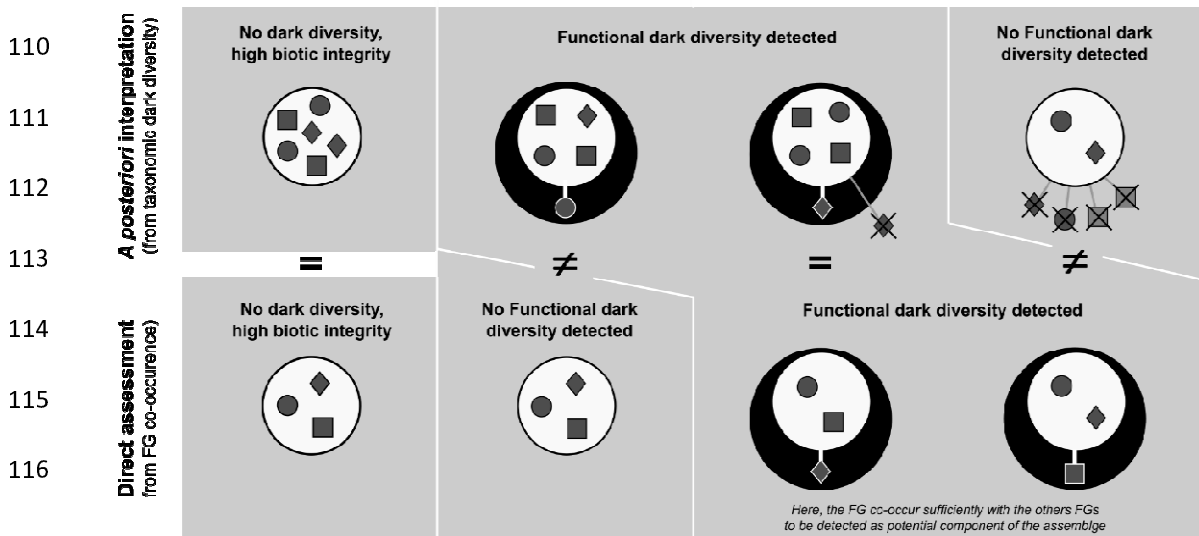
92 of community assembly, as well as the interest for conservation and the capacity of communities to
 93 be ecologically restored.



104 **Taxonomic dark diversity**



109 **Functional dark diversity**



117 **Figure 1.** Four distinct co-occurrence scenarios in several communities (a, b, c, d) from a single
118 habitat-specific species pool. The colour of drawing represent a species identity, and its shape
119 represent its functional group. From these local co-occurrences taken together, taxonomic dark
120 diversity and functional dark diversity can be estimated for the four communities. Functional dark
121 diversity estimated *a posteriori* (*i.e.* functional interpretation of taxonomic dark diversity) mirrors
122 taxonomic dark diversity, because it is only the translation into traits of the species which are lacking.
123 Functional dark diversity estimated *a priori* from the co-occurrence of functional groups differs from
124 taxonomic dark diversity and hence from functional dark diversity estimated *a posteriori*. In
125 particular, in the second community (b), a species is lacking, so its functional group seems also
126 lacking. However, this functional group is in fact already present in the community so cannot be
127 recruited. In the fourth community (d), many species are lacking but their co-occurrences with the
128 present species are too rare, so these species are not integrated into the taxonomic dark diversity.
129 However, the co-occurrence of their functional groups is frequent, thus the lacking functional group,
130 despite hosted by rare species, is integrated into the functional dark diversity calculated *a priori*.

131

132 While a functional interpretation of taxonomic dark diversity can be made *a posteriori* (*i.e.* what are
133 the traits of the species which are absent?), we think that the calculation of taxonomic dark diversity,
134 which is based in most cases on co-occurrence of species (Lewis, Szava-Kovats, & Pärtel, 2016), can in
135 itself limit the detection of functional patterns. Variations of taxonomic diversity have been shown to
136 often result from non-deterministic processes such as neutral coexistence (Chase & Leibold, 2003),
137 suggesting that taxonomic diversity could be a somewhat unreliable and unpredictable parameter,
138 influenced by stochastic processes. Moreover, taxonomic dark diversity taken alone can potentially
139 underestimate the ecological integrity of a community (*i.e.* the capacity of a community to harbour
140 species composition, diversity and functional organisation similar to those of undisturbed ecosystems
141 in the region) because it does not consider the functional redundancy within taxa and the niche filling
142 within habitats (Figure 1b). Most importantly, modern ecology has shown that, from an ecological
143 perspective, the coexistence of functional features, which can be traits or combinations of traits, is
144 much more informative and relevant than the coexistence of species (Mcgill, Enquist, Weiher, &
145 Westoby, 2006). What coexist are functional features, much more than truly independent species:
146 for plants, for example chamephytes, therophytes and small hemicryptophytes in peatlands,
147 helophytes and hydrophytes in marshes, woody species, shrubs, lianas and small herbs in forests...
148 Consequently, accounting for functional features in the co-occurrence calculation becomes a
149 necessity if we want to correctly infer from the concept of dark diversity the ecological determinants
150 of community assembly and identify the potential functions that can realistically be recruited in
151 natural communities, and thus, take fully appropriate conservation and restoration policies. Last, an
152 assessment of functional dark diversity through coexistence of functional features would also
153 increase the probability of detecting functional features hosted by rare species: the co-occurrences

154 of these species might be too rare for them to be included in the taxonomic dark diversity (so their
155 groups would not be included either with an *a posteriori* interpretation), but the co-occurrences of
156 their groups may be sufficiently frequent for the groups to be included in the functional dark
157 diversity (Figure 1d).

158 Terrestrial ecosystems currently experience many land-use changes, which raises important
159 questions about their impacts on biodiversity and natural habitats (Newbold et al., 2015). In
160 particular, how communities of ancient forests differ from those of recent woodlands is an old but
161 persistent issue of ecology (Bergès & Dupouey, 2020), which offers an ideal opportunity to make use
162 of dark diversity. Recent woodlands are spontaneous forests resulting from a secondary succession
163 following land abandonment, whereas ancient forests are uninterrupted forests since several
164 centuries (at least 150-400 years in western Europe, Hermy, Honnay, Firbank, Grashof-Bokdam, &
165 Lawesson, 1999). The interruption of forest temporal continuity generally induces two major
166 constraints for the forest re-assembly: recruitment limitation and dispersal limitation, respectively
167 due to past land-uses (e.g. fertilisation or soil disturbance) and spatio-temporal fragmentation of
168 source habitats (Hermy & Verheyen, 2007; Kimberley, Blackburn, Whyatt, Kirby, & Smart, 2013).
169 Consequently, the composition and structure of communities in recent woodlands often differ
170 strongly from those of ancient forests. Notably, recent woodlands often lack specialised, typical plant
171 species of ancient forests, which are characterised by low seed production, low dispersal capacities,
172 and require very precise ecological conditions such as oligotrophic substrates and soils weakly
173 disturbed (Flinn & Vellend, 2005). Animal groups may also be sensitive to the forest temporal
174 continuity, in particular arthropods, which are highly dependent to local habitat conditions
175 (Hofmeister et al., 2019). Among arthropods, spiders might be particularly interesting to survey
176 because they are ubiquitous in all terrestrial ecosystems, and the structure of their community might
177 be gradually reshaped during the successional trajectory (Morel et al., 2019; Oxbrough, Gittings,
178 O'Halloran, Giller, & Smith, 2005). Overall, many aspects of the ecological consequences of the
179 rupture of forest temporal continuity remain to be deepened, for instance the relative importance of
180 dispersal and recruitment limitations on biodiversity recovering, which is highly context-dependant
181 (see Bergès & Dupouey, 2020). Thus, the application of the dark diversity framework should enable
182 to obtain a more realistic vision of the capacities of ecosystems to spontaneously recover
183 biodiversity.

184 Here, we developed the first method to estimate functional dark diversity, and we applied this
185 method to evaluate how passive rewilding (*i.e.* spontaneous afforestation) may reshape the
186 biocenosis of forest ecosystems. We sampled plant and spider communities, two main understory
187 taxas which depend on distinct biotic and abiotic conditions, and characterised their spectrum of

188 functional traits. We calculated taxonomic dark diversity using the species co-occurrence method
189 (Lewis et al., 2016) and adapted this method to assess functional dark diversity, using co-occurrence
190 of functional groups, which were identified through multitrait differences. Then, we compared recent
191 woodlands with ancient forests. We tested the following hypotheses: (i) the composition of
192 functional dark diversity is specific to the forest type, illustrating their different ecological
193 constraints, (ii) recent woodlands harbour plant and spider communities with both higher taxonomic
194 and functional dark diversity than ancient forests (*i.e.* restoration is partially effective) and (iii)
195 functional dark diversity does not equate to taxonomic dark diversity.

196

197 **Materials and methods**

198 *Study sites*

199 We conducted the study in different forest environments of Western Europe (Brittany, France). We
200 selected 32 plots of mesophilic, oak and beech-dominated mature forests, within sites sharing similar
201 geological substrates (mainly granite rocks and schists), thereby strongly limiting the influence of
202 environmental heterogeneity and stand maturity. These plots were homogeneous management units
203 of around 1 ha and were distributed across 8 sites (ranging from 200 to 4000 ha) within the regional
204 area. We set apart plots of ancient forests from those of recent woodlands by checking the temporal
205 forest continuity thanks to the historical Cassini map layers (year 1790) and the Napoleonic cadastre
206 (year 1847), that is, the two reference documents in France for the historical land-uses (Cateau et al.,
207 2015). We defined ancient forests as sites already forested in the middle of the 18th century (when
208 the overall forested area was at its minimum over the French territory, Cateau et al., 2015) and
209 recent woodlands as forests resulting from farmland abandonment during the 20th century.
210 Therefore, ancient forests have an uninterrupted forest state since at least 230 years and recent
211 woodlands are not older than 120 years. Our dataset included 20 plots in ancient forests (from six
212 different forest sites) and 12 plots in recent woodlands (from two different forest sites). The habitat
213 structure and the ecological conditions were quite similar between recent and ancient forests: there
214 were no differences of canopy cover, basal area and Ellenberg Indicator Values (EIV) for moisture
215 degree (Table S1). But, EIV showed higher pH, nutrient concentration and shading in recent
216 woodlands in comparison to ancient forests (Table S1), which is consistent with previous studies
217 investigating environmental conditions in post-agricultural woodlands (Koerner, Dupouey, Dambrine,
218 & Benoit, 1997).

219

220 *Community sampling*

221 We conducted floristic surveys in June-July 2014 and 2015 to sample the understorey plant
222 communities of the selected plots (*i.e.* below 2 meters high and including woody species). We used
223 50-m² quadrats (10 x 5 m) and we noted all species encountered belonging to the herbaceous and
224 shrub strata. A total of 99 species was recorded.

225 To sample spider communities, we compiled data from a regional database which included individual
226 sampling conducted within the same 32 plots that we used for the floristic surveys. Sampling was
227 made using a standardised protocol based on 3 pitfall traps spaced 10m apart and located at the
228 centre of the plot. Sampling was conducted between April and June either in 2013, 2014, or 2015
229 (see Morel et al., 2019 and references for database description and more details on the sampling
230 method). The final dataset included 3615 adult individuals, belonging to 89 species.

231 *Functional characterisation of species*

232 We selected 9 functional traits from the LEDA database (Kleyer et al., 2008) to measure the
233 functional variability of plant species. These traits relate to the plants' ecological strategy for
234 resource acquisition, competition, regeneration and dispersal (Table S2). We selected two traits of
235 the leaf economics spectrum (Wright et al., 2004) informing about resource acquisition, resource
236 conservation and competition: the specific leaf area (SLA) and the leaf dry matter content (LDMC).
237 We selected four regenerative traits related to growth and dispersal in space and time (Pérez-
238 Harguindeguy et al., 2013): dispersal syndrome, pollination type, seed dry mass and start of
239 flowering. We also selected two integrative traits informing about the overall ecological strategy of
240 plants: plant height and life form. All of these traits are response-effect traits (Lavorel & Garnier,
241 2002) since they both respond to environmental conditions and also influence ecosystem functions.
242 Since traits were not overly correlated (all $r < 0.60$), we kept the 9 selected traits. The dataset
243 comprised 16 missing values, that is, 1.8% of the dataset.

244 We selected 4 life-history traits available in the literature to characterise the functional variability of
245 spider species (Table S3): body size, guild, phenology and circadian activity. These traits relate to the
246 ecological strategy of spiders, in particular their diet and hunting specialisation, foraging method, the
247 habitats they exploit and their dispersal abilities. They hence represent key features illustrating the
248 assemblages of predator arthropods at local scale (Cardoso, Pekár, Jocqué, & Coddington, 2011).

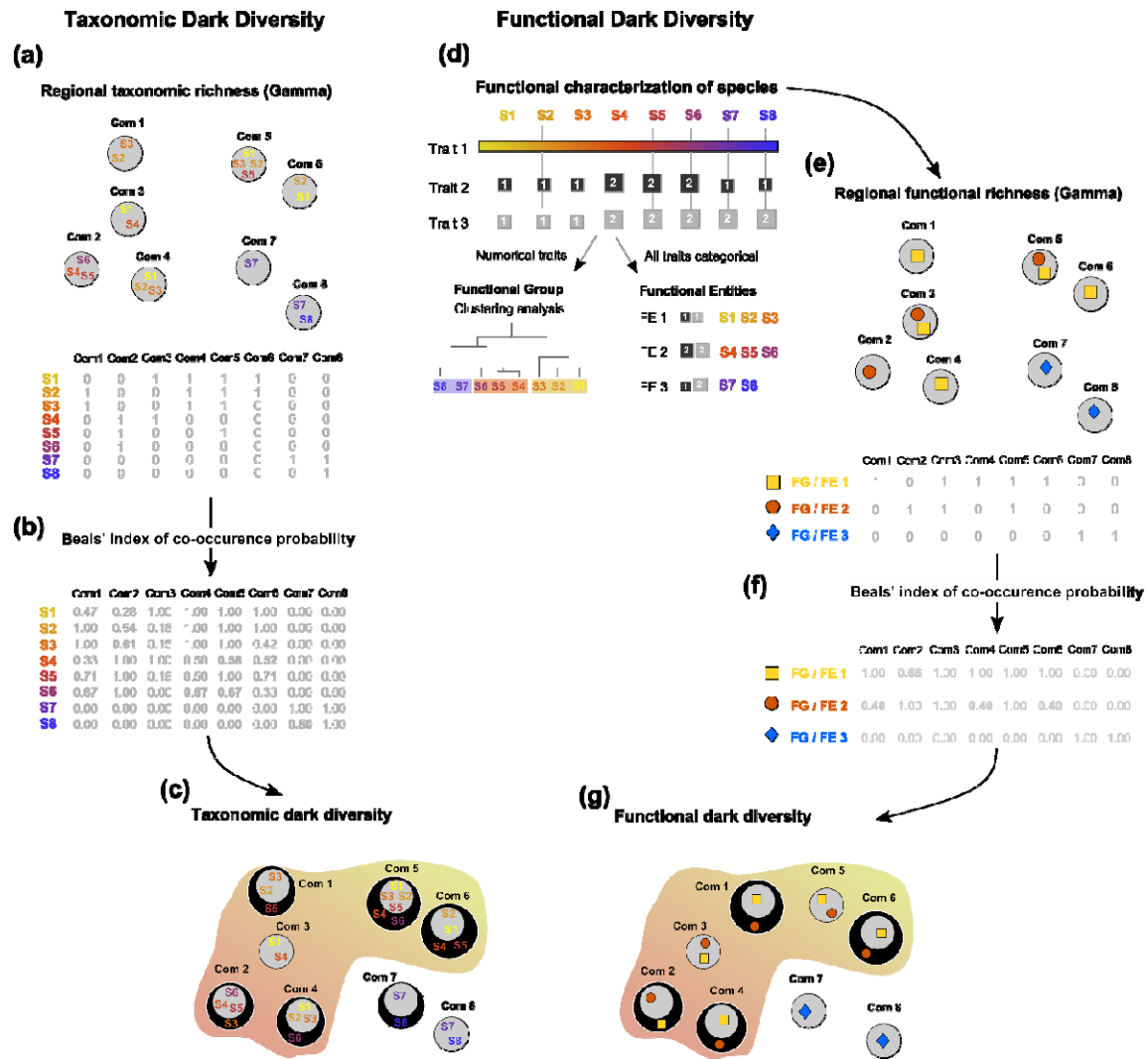
249 *Identification of functional groups*

250 Since we aimed at using a co-occurrence index to calculate functional dark diversity, we needed to
251 divide the species pool into discontinuous elements, that is, functional groups. For plants, we divided

252 the species pool into functional groups following the methods of Verheyen, Honnay, Motzkin, Hermy,
253 & Foster (2003), which were used in a similar investigation of recent versus ancient understorey
254 plant communities. This method allows to identify functional groups according to trait correlations
255 and thus select objectively consistent ecological groups. First, we calculated a species-to-species
256 distance matrix with the Gower's similarity coefficient, since this coefficient can deal with missing
257 values and both quantitative and qualitative data. Then, we used this matrix to cluster the species
258 into functional groups using the Ward's method (Murtagh & Legendre, 2014). The optimal number of
259 groups was determined graphically from visual screening of the dendrogram (Figure S1). We
260 identified 10 functional groups of plant species: 4 groups of woody plants and 6 groups of
261 herbaceous and graminoid species (Figure S1). We made sure that the selected groups were
262 ecologically relevant, that is, corresponded to subsets that were noticeable on the field. For spiders,
263 we applied the method of functional entities since all traits were categorical, and each unique
264 combination of traits resulted in a distinct group (Mouillot et al., 2014). Thus, we identified 35
265 functional entities (Table S4). We run the further analyses with these groups for plants and spiders,
266 but note that we also run the analyses with groups defined *a priori*, to ensure that our results were
267 not trivially the reflection of group selection. For plants, we adapted the "biological types" of species
268 recorded in the French flora database (Baseflor; Julve, 1998), which are derived from the
269 classification of Raunkier, and we partitioned the species into 12 groups. For spiders, we used the
270 guilds' typology developed by Cardoso et al. (2011), and we partitioned the species into 7 groups.
271 With this alternative group selection, we obtained the same results hereafter for both plants and
272 spiders (Figure S2).

273 *Measuring dark diversity and completeness*

274 First of all, we measured the taxonomic and functional, observed diversity of communities (see Table
275 S5). Then, we calculated dark diversity using the Beals' co-occurrence index (Beals, 1984), a method
276 considered by Lewis et al. (2016) as one of the most efficient. This method relies on a calculus of co-
277 occurrence that enables to identify the subset of species that have the greatest probabilities to
278 coexist, within the habitat-specific species pool that was defined as our whole dataset. In a given
279 community, the taxonomic dark diversity integrates species that are absent but have the greatest
280 probabilities to coexist with the present species (Figure 2). We calculated taxonomic dark diversity
281 according to this method, using a significance threshold of 0.05, as advised by (Lewis et al., 2016).



282

283 **Figure 2.** Analysis approach for measuring taxonomic and functional dark diversity. “Com1” means
 284 community 1 and “S1” means species 1. (a) From the species’ presence/absence matrix, (b) the Beals’
 285 index estimates the co-occurrence probability of each species in each community. (c) In a given
 286 community, a missing species having a high co-occurrence probability in this community will be
 287 integrated to the taxonomic dark diversity of this community. The methodological principle for
 288 measuring functional dark diversity is identical (e, f, g), but the Beals’ index relies on a matrix of
 289 functional groups (or functional entities), preliminary obtained from the functional character
 290 of species (d). In (c) and (g), the dark diversity of each community is represented by a circle with a
 291 black background surrounding the communities with their observed diversity.

292

293 Then, we adapted this method to calculate functional dark diversity: instead of using taxonomic co-
 294 occurrence, we used functional co-occurrence, that is, the probability of functional groups or
 295 functional entities to coexist (Figure 2). The rest of the procedure was identical: we identified in each
 296 community the functional groups that were absent while they have an important probability to

297 coexist with the functional groups present in the community. We also calculated a percentage of
298 change between recent and ancient forest for each species and each functional group identified in
299 the dark diversity. Finally, to avoid biased interpretations of the differences in dark diversity due to
300 variations in species richness, we calculated the functional completeness of communities (Pärtel,
301 Szava-Kovats, & Zobel, 2013), that is, their observed diversity relative to their dark diversity. We used
302 the formula: $\ln \left(\frac{\text{observed diversity}}{\text{dark diversity}} \right)$. The numerator and denominator were increased by 1 to avoid
303 the limits of division by zero (Helm, Zobel, Moles, Szava-Kovats, & Pärtel, 2015).

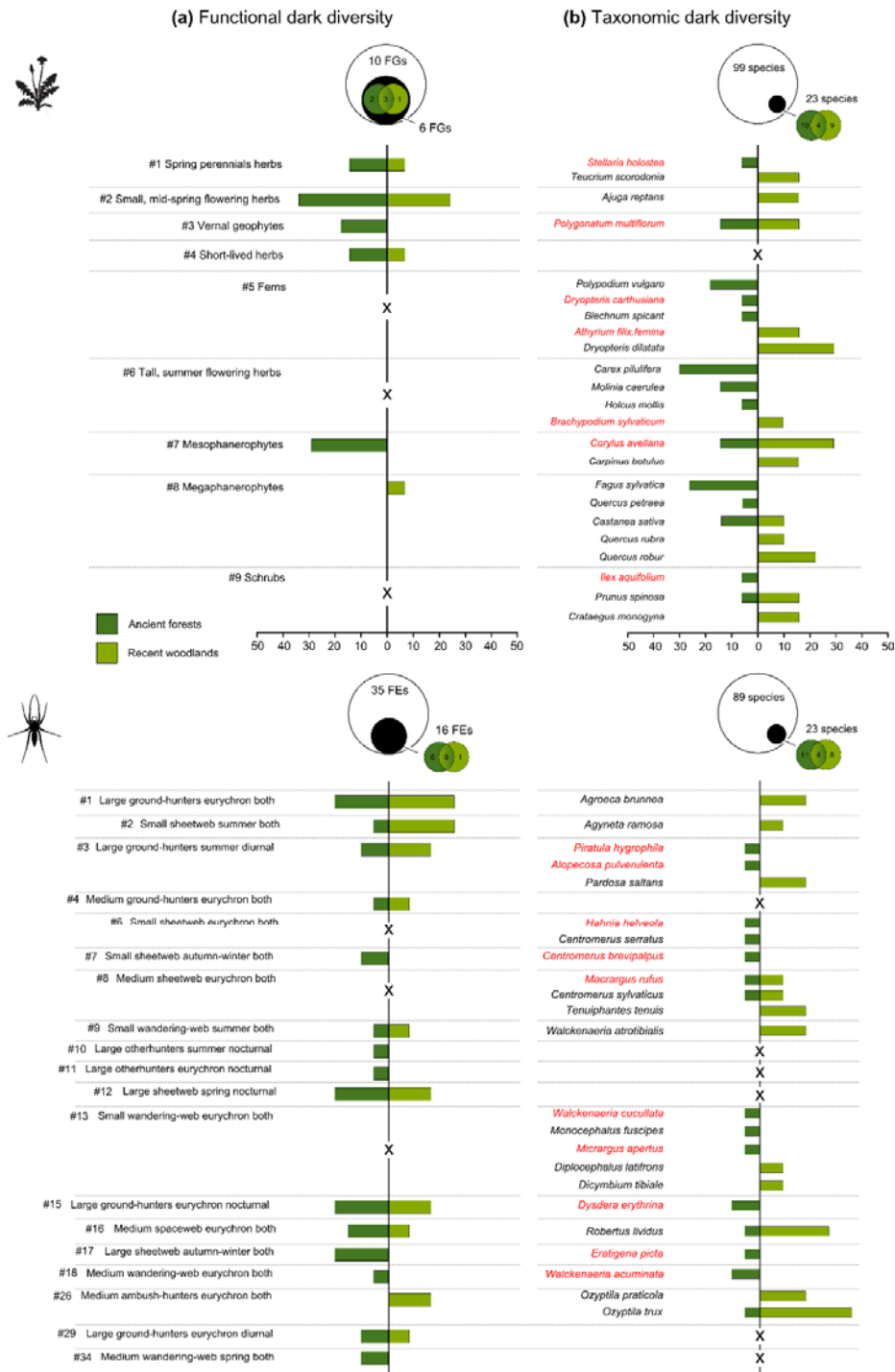
304 *Data analysis*

305 We had a dataset with a nested structure: replicate plots nested into forest plots, nested into forest
306 types. Therefore, we used generalised linear mixed models (GLMMs with Poisson distribution family)
307 for discrete variables (dark diversity) and linear mixed models (LMMs) for continuous variables
308 (completeness) to test differences among forest types (*i.e.* ancient versus recent). We used the forest
309 type as a fixed factor and the hierarchical structure (plots nested within sites) as a random effect, to
310 remove any potential effect of autocorrelation. All analyses were performed using R software (R core
311 team, 2017). The handling of trait matrices and identification of functional groups were done using
312 the package “cluster” and the “species_to_FE” and “FE_metrics” functions (Mouillot et al., 2014). The
313 measures of dark diversity were made with the package “vegan” and the “beals” function, and the
314 script provided by Lewis et al. (2016). Statistical tests were performed thanks to the package “lme4”.

315 **Results**

316 *Composition of dark diversity in ancient and recent forests*

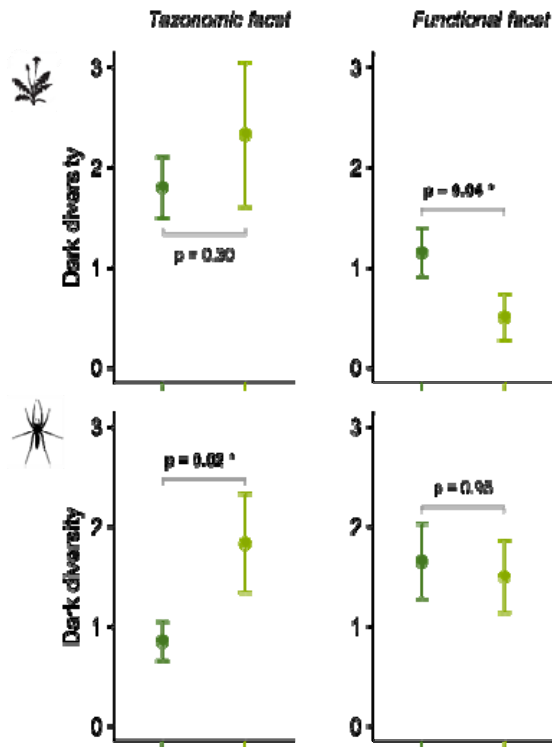
317 The composition of taxonomic and functional dark diversity strongly differed between both forest
318 types. Only 4 plant species, 4 spider species, 3 plant functional groups and 9 spider functional entities
319 were observed in the dark diversity of both forest types. In the other hand, 10 plant species and two
320 plant functional groups (mesophanerophytes and vernal geophytes) were specific to the dark
321 diversity of ancient forests (Figure 3), whereas 9 plant species and one plant functional group
322 (megaphanerophytes) were specific to the dark diversity of recent forests (Figure 3). Furthermore, 11
323 spider species and 6 spider functional entities were specific to the dark diversity of ancient forests
324 and 8 spider species and one spider functional entity were specific to the dark diversity of recent
325 forests (Figure 3). Last, we observed that some species were present in the taxonomic dark diversity
326 while their groups were absent in the functional dark diversity, and conversely (Figure 3).



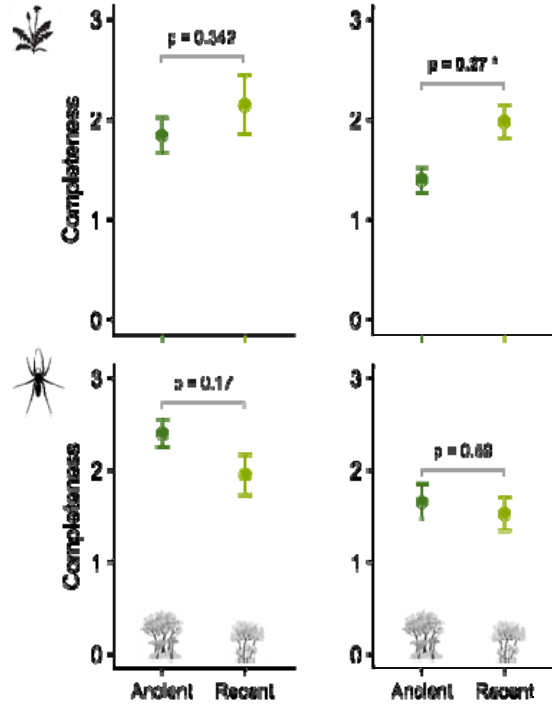
327

328 **Figure 3.** Occurrence frequency in the dark diversity of ancient and recent forests of (a) functional
 329 groups (FGs) of plants and functional entities (FEs) of spiders and (b) species of plants and spiders.
 330 Only groups, entities and species observed at least once in the dark diversity are presented. Species
 331 usually more frequent in ancient forests are in red (from Hermy et al., 1999 and Morel et al., 2019 for
 332 plants and spiders, respectively). Black crosses indicate absence in the dark diversity. See Figure S1
 333 and Table S4 for more details on functional groups and entities. Also, see Table S5 for compare
 334 species and FG/FE occurrence frequency in observed diversity.

(a) Dark diversity



(b) Completeness



335

336

337 **Figure 4.** Comparisons of dark diversity (a) and completeness (b) between ancient and recent forests,
338 for plant and spider communities, and for the taxonomic and the functional facets (n=32).

339 *Taxonomic and functional dark diversity in ancient and recent forests*

340 In total, 23 plant species (23% of the species pool) and 23 spider species (26% of the species pool)
341 were recorded at least once in the taxonomic dark diversity (Figure 3). Also, 6 functional groups of
342 plants (60% of the pool of functional groups) and 16 functional entities of spiders (46% of the pool of
343 functional entities) were recorded at least once in the functional dark diversity (Figure 3).

344 Overall, we found differences in taxonomic and functional dark diversity between ancient and recent
345 forests (Figure 4a). We found these differences were opposite for taxonomic and functional dark
346 diversity, both in sign and magnitude. For plants, there was similar taxonomic dark diversity in
347 ancient and recent forests (2.3 ± 2.5 vs. 1.8 ± 1.4 , $p > 0.05$, Wald's test) but more functional dark
348 diversity in ancient forests (1.2 ± 1.1 vs. 0.5 ± 0.8 , $p < 0.05$, Wald's test). For spiders, there were more
349 taxonomic dark diversity in recent forests than in ancient ones (1.8 ± 1.7 vs. 0.9 ± 0.9 , $p < 0.05$, Wald's
350 test), but similar functional dark diversity (1.5 ± 1.2 vs. 1.7 ± 1.7 , $p > 0.05$, Wald's test). Last, the
351 completeness of recent woodlands was higher than that of ancient forests concerning plant
352 functional group, and similar concerning spider functional entities (Figure 4b).

353 **Discussion**

354 Our application of the dark diversity framework into a case study of passive rewilding revealed
355 several novel ecological insights concerning the mechanisms involved in the re-assembly of natural
356 communities during land-use changes. Moreover, the direct quantification of functional dark
357 diversity brought new light on the potential abilities of recent woodlands to spontaneously
358 recovering native forest biodiversity. We thus demonstrated that, surprisingly, recent forests were in
359 fact quite complete from an overall, ecological perspective. Despite lacking specialist, plant and
360 spider species, recent woodlands already harboured functionally rich communities.

361 *Taxonomic and functional dark diversity: two distinct but complementary facets of potential*
362 *biodiversity*

363 Our results obtained from functional dark diversity clearly differed from those obtained from
364 taxonomic dark diversity, both in terms of quality (*i.e.* composition of dark diversity) and quantity
365 (*i.e.* amount of dark diversity). For plants and spiders, the taxonomical approach integrated only one
366 quarter of all species into dark diversity, whereas about half of all functional groups were integrated
367 at least once into functional dark diversity. Thus, our results suggest that an exclusively taxonomic
368 approach tends in fact to overestimate the ecological integrity of communities, by missing out the
369 fact that some niches are actually vacant in several communities. By focusing on the co-occurrence of
370 functional groups rather than co-occurrence of species, and considering that *any* species of a given

371 lacking group could be recruited, our approach enabled to identify vacant niches even when the
372 species of the group concerned were not integrated into taxonomic dark diversity. For example, no
373 species of short-lived herbs (FG #4) or medium-size generalist hunting spiders (FE #4) was ever
374 integrated into taxonomic dark diversity, while these groups were often integrated into functional
375 dark diversity (Figure 3). We thus note that our approach increased the probability of detecting the
376 absence of functional features hosted by several rare species, whereas neither taxonomic dark
377 diversity nor a functional interpretation of it could detect them (as we assumed, see Figure 1d).

378 On the other hand, functional dark diversity as we calculated it might, too, overestimate the
379 ecological integrity of natural communities, because it considers communities represented by a
380 single species per group as complete (see Figure 1b). Thus, species may be lacking but their
381 respective groups may not: for example, shrubs and ferns were never included into dark diversity,
382 whereas some of their species were (Figure 3). We could hence summarise our approach in simple
383 words: functional dark diversity is not interested in species. This can be a major advantage: for
384 habitat conservation and restoration, it is often crucial to investigate ecosystem functioning and
385 related services before assessing their richness or originality in species (Cadotte, Carscadden, &
386 Mirotchnick, 2011). However, this could be a drawback in other cases: conservation and restoration
387 policies can also target species for their intrinsic patrimonial value (e.g. existence values), hence
388 requiring consideration of species. Rare species may also play a key role in ecosystem functioning by
389 ensuring singular functions or enhancing functional redundancy (Chapman, Tunnicliffe, & Bates,
390 2018; Leitão et al., 2016). We hence suggest that further methods need to be developed to measure
391 the potential regeneration of natural habitats considering rare species with rare functional features.
392 Overall, we think that taxonomic dark diversity and functional dark diversity illustrate different facets
393 of communities, and that they can be very complementary metrics which, taken together, provide
394 reliable information for ecological diagnostic and for conservation and restoration policies.

395 *Dark diversity brings to light recruitment limitations during the forest recovering process but with*
396 *little impact on forest functional integrity*

397 Our results confirmed that recent woodlands, even after decades of forest re-establishing, do not
398 fully recover communities like those of ancient forests in terms of species identity, whether for
399 plants (Bergès & Dupouey, 2020; Hermy & Verheyen, 2007) or spiders (Morel et al., 2019). Dark
400 diversity showed that recent forests mainly lacked some generalist species they could recruit (e.g.
401 phanerophytes or ruderal-nitrophilous plants such as *Crataegus monogyna* and *Ajuga reptans*, and
402 several ubiquitous hunter spiders such as *Agroeca brunnea* and *Pardosa saltans*). Moreover, we
403 observed that recent forests also lacked specialist forest species, but they might not be able to be

404 recruited, since they were not identified in dark diversity. These specialists, which are mainly slow-
405 colonisers associated with specific, restricted ecological conditions (e.g. oligotrophic and acidophil
406 soils for plants, Hermy & Verheyen, 2007, and complex litters associated to dead-wood materials for
407 spiders, Morel et al., 2019) were almost exclusively associated, when they were absent, to ancient
408 forests. Therefore, all these compositional differences in the dark diversity suggest that a recruitment
409 limitation due to past land-uses was, here, the main driver of the reshaping of communities, rather
410 than a dispersal limitation.

411 Beyond these changes in species identities, dark diversity also showed that recent woodlands
412 harboured diverse communities which were quite complete from a functional perspective, especially
413 regarding plants. Recent woodlands mainly lacked small springs herbs whereas ancient forests also
414 lacked shrubs, vernal geophytes and various herbs. Three complementary hypotheses could explain
415 this result. First, recent woodlands might temporary harbour "relictual species" (and their functional
416 features) inherited from preceding successional stages (e.g. shrubs species), which might be in
417 extinction debt and could disappear with time (Bagaria, Helm, Rodà, & Pino, 2015). Second, past land
418 uses may have reduced nutrient limitation through soil fertilisation, particularly on the acid soils of
419 our study region (Graae, 2000; Koerner et al., 1997), leading to recruitment of more diverse
420 functional features in recent woodlands (Morel et al., 2019b). Last, past management of forests
421 might also play a role: since several centuries, the management of ancient forests has shifted from
422 coppicing to high-forest system, which has tended to disadvantage shade-loving, understorey woody
423 and herb species (Kirby & Watkins, 2015). On the contrary, recent woodlands conserve a denser
424 coppice, thus leading to a lower amount of light reaching their understorey (illustrated by the
425 Ellenberg values, Table S1), which could enrich the herbaceous cover in both species and functional
426 plant features. According to these last two hypotheses, compositional differences between both
427 forest types should be maintained with time.

428 Overall, we believe that our results may challenge and improve our perception of the conservation
429 value of both recent and ancient forests: recent woodlands do lack typical ancient forest species, but
430 they can also recover functionally rich and ecologically complete communities. Even if forestry is not
431 incompatible with biodiversity, we think that an increase in wildwood areas could benefit to
432 conservation of forest ecosystems.

433 *Perspectives and limitations*

434 We argue for the development of the framework of functional dark diversity for both researchers
435 and practitioners, notably in the study of biodiversity responses to land-use changes. First, we
436 acknowledge some limitations of our results: our recent study forests might be in somewhat good

437 conditions compared to other ones elsewhere in the study region, because they have not undergone
438 a particularly excessive anthropogenic pressure during their regeneration. We also note that we
439 studied dark diversity on a relatively small dataset (*i.e.* several forests of Brittany), but we think it
440 was sufficiently robust to analyse the different facets of dark diversity and test their dissemblances.
441 In addition, the fact that both compositional and diversity patterns are congruent between the two
442 distinct taxa studied (especially in term of functional integrity within recent woodlands), tends to
443 confirm the robustness of our results. Overall, we think that our method assessing functional dark
444 diversity, with its simplicity, can easily be applied to many other issues of conservation and
445 restoration. The combined use of functional and taxonomic dark diversity can deal with the
446 assessment of the ecological integrity of natural communities, both from a functional perspective
447 (including resistance and resilience capacities of ecosystems) and from a taxonomic one (e.g.
448 recruitment of species with particular interest). Since the method is entirely based on the co-
449 occurrence of functional groups, the choice of these functional groups is a central concern. We
450 ensured that functional groups satisfied two conditions: functional redundancy had to be higher
451 within groups than between groups, and coexistence within groups had to be neutralist. We also
452 ensured that the selected functional groups corresponded to a precise ecological compartment, that
453 is, a subset of species that was noticeable in the field. In this way, we think that the functional group
454 approach for dark diversity may be used, and does have a biological sense. Further methods could be
455 developed in the future, using a continuous approach for traits along the whole calculation process,
456 or focusing on the specialisation degree, the evolutionary distinctiveness or the functional originality
457 of species present in the dark diversity.

458 **References**

- 459 Bagaria, G., Helm, A., Rodà, F., & Pino, J. (2015). Assessing coexisting plant extinction debt and
460 colonization credit in a grassland–forest change gradient. *Oecologia*, 179(3), 823–834.
- 461 Beals, A. (1984). Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological
462 data. *Advances in Ecological Research*, 14, 1–55.
- 463 Bergès, L., & Dupouey, J. (2020). Historical ecology and ancient forests: Progress, conservation issues
464 and scientific prospects, with some examples from the French case. *Journal of Vegetation*
465 *Science*, jvs.12846.

- 466 Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: functional diversity and
467 the maintenance of ecological processes and services: Functional diversity in ecology and
468 conservation. *Journal of Applied Ecology*, 48(5), 1079–1087.
- 469 Cardoso, P., Pekár, S., Jocqué, R., & Coddington, J. A. (2011). Global Patterns of Guild Composition
470 and Functional Diversity of Spiders. *PLoS ONE*, 6(6), e21710. doi:
471 10.1371/journal.pone.0021710
- 472 Cateau, E., Larrieu, L., Vallauri, D., Savoie, J.-M., Touroult, J., & Brustel, H. (2015). Ancienneté et
473 maturité: deux qualités complémentaires d'un écosystème forestier. *Comptes Rendus
474 Biologies*, 338(1), 58–73.
- 475 Chapman, A. S. A., Tunnicliffe, V., & Bates, A. E. (2018). Both rare and common species make unique
476 contributions to functional diversity in an ecosystem unaffected by human activities.
477 *Diversity and Distributions*, 24(5), 568–578.
- 478 Chase, J. M., & Leibold, M. A. (2003). *Ecological niches: linking classical and contemporary
479 approaches*. Chicago: University of Chicago Press.
- 480 Flinn, K. M., & Vellend, M. (2005). Recovery of forest plant communities in post-agricultural
481 landscapes. *Frontiers in Ecology and the Environment*, 3(5), 243–250.
- 482 Graae, B. J. (2000). The effect of landscape fragmentation and forest continuity on forest floor
483 species in two regions of Denmark. *Journal of Vegetation Science*, 11(6), 881–892.
- 484 Helm, A., Zobel, M., Moles, A. T., Szava-Kovats, R., & Pärtel, M. (2015). Characteristic and derived
485 diversity: implementing the species pool concept to quantify conservation condition of
486 habitats. *Diversity and Distributions*, 21(6), 711–721.
- 487 Hermant, M., Hennion, F., Bartish, I., Yguel, B., & Prinzing, A. (2012). Disparate relatives: Life histories
488 vary more in genera occupying intermediate environments. *Perspectives in Plant Ecology,
489 Evolution and Systematics*, 14, 283–301.
- 490 Hermy, M., & Verheyen, K. (Eds.). (2007). Legacies of the past in the present-day forest biodiversity: a
491 review of past land-use effects on forest plant species composition and diversity. In

- 492 *Sustainability and Diversity of Forest Ecosystems: an Interdisciplinary Approach* (pp. 361–
493 371). Tokyo; New York: Springer.
- 494 Hermy, Martin, Honnay, O., Firbank, L., Grashof-Bokdam, C., & Lawesson, J. E. (1999). An ecological
495 comparison between ancient and other forest plant species of Europe, and the implications
496 for forest conservation. *Biological Conservation*, *91*(1), 9–22.
- 497 Heister, J., Hošek, J., Brabec, M., Hermy, M., Dvořák, D., Fellner, R., ... Kadlec, T. (2019) Shared affinity
498 of various forest-dwelling taxa point to the continuity of temperate forests. *Ecological*
499 *Indicators*, *101*, 904-912.
- 500 Jackson, S. T., & Sax, D. F. (2010). Balancing biodiversity in a changing environment: extinction debt,
501 immigration credit and species turnover. *Trends in Ecology & Evolution*, *25*(3), 153–160.
- 502 Julve, P. (1998). *Baseflor: index botanique, écologique et chorologique de la flore de France*. Institut
503 Catholique de Lille.
- 504 Kimberley, A., Blackburn, G. A., Whyatt, J. D., Kirby, K., & Smart, S. M. (2013). Identifying the trait
505 syndromes of conservation indicator species: how distinct are British ancient woodland
506 indicator plants from other woodland species? *Applied Vegetation Science*, *16*(4), 667–675.
- 507 Kirby, K., Watkins, C., 2015. Europe's Changing Woods and Forests: From Wildwood to Managed
508 Landscapes. CABI, 363p.
- 509 Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., ... Peco, B.
510 (2008). The LEDA Traitbase: a database of life-history traits of the Northwest European flora.
511 *Journal of Ecology*, *96*(6), 1266–1274.
- 512 Koerner, W., Dupouey, J. L., Dambrine, E., & Benoit, M. (1997). Influence of Past Land Use on the
513 Vegetation and Soils of Present Day Forest in the Vosges Mountains, France. *The Journal of*
514 *Ecology*, *85*(3), 351.
- 515 Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem
516 functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, *16*(5), 545–556.

- 517 Leitão, R. P., Zuanon, J., Villéger, S., Williams, S. E., Baraloto, C., Fortunel, C., ... Mouillot, D. (2016).
518 Rare species contribute disproportionately to the functional structure of species
519 assemblages. *Proceedings of the Royal Society B: Biological Sciences*, 283(1828), 20160084.
- 520 Lewis, R. J., de Bello, F., Bennett, J. A., Fibich, P., Finerty, G. E., Götzenberger, L., ... Pärtel, M. (2017).
521 Applying the dark diversity concept to nature conservation: Dark Diversity and Nature
522 Conservation. *Conservation Biology*, 31(1), 40–47.
- 523 Lewis, R. J., Szava-Kovats, R., & Pärtel, M. (2016). Estimating dark diversity and species pools: an
524 empirical assessment of two methods. *Methods in Ecology and Evolution*, 7(1), 104–113.
- 525 McGill, B., Enquist, B., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from
526 functional traits. *Trends in Ecology & Evolution*, 21(4), 178–185.
- 527 Moeslund, J. E., Brunbjerg, A. K., Clausen, K. K., Dalby, L., Fløjgaard, C., Juel, A., & Lenoir, J. (2017).
528 Using dark diversity and plant characteristics to guide conservation and restoration. *Journal*
529 *of Applied Ecology*, 54(6), 1730–1741.
- 530 Morel, L., Dujol, B., Courtial, C., Vasseur, M., Leroy, B., & Ysnel, F. (2019a). Spontaneous recovery of
531 functional diversity and rarity of ground-living spiders shed light on the conservation
532 importance of recent woodlands. *Biodiversity and Conservation*, 28(3), 687–709.
- 533 Morel, L., Barbe, L., Jung, V., Clément, B., Schnitzler, A. & Ysnel, F. (2019b). Passive rewilding may
534 (also) restore phylogenetically rich and functionally resilient forest plant communities.
535 *Ecological Applications*, 30(1), e02007.
- 536 Mouillot, D., Villegier, S., Parravicini, V., Kulbicki, M., Arias-Gonzalez, J. E., Bender, M., ... Bellwood, D.
537 R. (2014). Functional over-redundancy and high functional vulnerability in global fish faunas
538 on tropical reefs. *Proceedings of the National Academy of Sciences*, 111(38), 13757–13762.
- 539 Murtagh, F., & Legendre, P. (2014). Ward's Hierarchical Agglomerative Clustering Method: Which
540 Algorithms Implement Ward's Criterion? *Journal of Classification*, 31(3), 274–295.
- 541 Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., ... Purvis, A. (2015). Global
542 effects of land use on local terrestrial biodiversity. *Nature*, 520(7545), 45–50.

- 543 Oxbrough, A. G., Gittings, T., O'Halloran, J., Giller, P. S., & Smith, G. F. (2005). Structural indicators of
544 spider communities across the forest plantation cycle. *Forest Ecology and Management*,
545 *212*(1–3), 171–183.
- 546 Pärtel, M. (2014). Community ecology of absent species: hidden and dark diversity. *Journal of*
547 *Vegetation Science*, *25*(5), 1154–1159.
- 548 Pärtel, M., Szava-Kovats, R., & Zobel, M. (2011). Dark diversity: shedding light on absent species.
549 *Trends in Ecology & Evolution*, *26*(3), 124–128.
- 550 Pärtel, M., Szava-Kovats, R., & Zobel, M. (2013). Community Completeness: Linking Local and Dark
551 Diversity within the Species Pool Concept. *Folia Geobotanica*, *48*(3), 307–317.
- 552 Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., ... Cornelissen,
553 J. H. C. (2013). New handbook for standardised measurement of plant functional traits
554 worldwide. *Australian Journal of Botany*, *61*(3), 167.
- 555 Prinzing, A., Reiffers, R., Braakhekke, W. G., Hennekens, S. M., Tackenberg, O., Ozinga, W. A., ... van
556 Groenendael, J. M. (2008). Less lineages more trait variation: phylogenetically clustered plant
557 communities are functionally more diverse. *Ecology Letters*, *11*(8), 809–819.
- 558 Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., & Foster, D. R. (2003). Response of forest plant
559 species to land-use change: a life-history trait-based approach. *Journal of Ecology*, *91*(4),
560 563–577.
- 561 Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the
562 concept of trait be functional! *Oikos*, *116*(5), 882–892.
- 563 Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... others. (2004). The
564 worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827.
- 565 Core Team (2017). R: A language and environment for statistical computing. R Foundation for
566 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 567
- 568

569 **Supplementary Information**

570 **Table S1.** Mean values of environmental parameters in recent woodlands and ancient forests (mean
571 \pm standard deviation). Habitat structure was assessed from canopy cover (visual vertical estimation
572 above each plot) and basal area (measured with a chain-relascope). We infer abiotic conditions from
573 Ellenberg Indicator Values (EIV) for moisture, reaction, nitrogen and light, using flora data adapted to
574 the Western Europe flora (Hill 1999). EIV were weighted by the vegetation cover (in %) to account for
575 species abundances. We determined differences using Student tests.

	Recent woodlands	Ancient forests	<i>p</i> -value
<i>n</i> plots	12	20	
Habitat structure			
Canopy cover (%)	74.6 \pm 3.1	77.3 \pm 3.1	0.549
Basal area (m ² ha ⁻¹)	27.6 \pm 1.9	31.1 \pm 1.9	0.217
Ellenberg Indicator Value (EIV)			
Moisture (F)	5.65 \pm 0.04	5.62 \pm 0.04	0.54
Reaction (R)	5.93 \pm 0.08	4.62 \pm 0.1	< 0.001
Nitrogen (N)	5.72 \pm 0.06	4.52 \pm 0.1	< 0.001
Light (L)	5.12 \pm 0.08	5.42 \pm 0.06	0.008

576

577 Hill, M.O., 1999. Ellenberg's Indicator Values for British Plants. DETR, Rotherham.

578

579

580

581

582

583

584

585 **Table S2.** Description of functional traits used to characterise plant species, from the LEDA database.

586 Trait types: 1=quantitative, 2=qualitative, 3=ordinal.

	Functional traits	Type	Description and units
1	Dispersal syndrome 99 (100%)	2	Anemochory; autochory; barochory; hydrochory; endozoochory; epizoochory and myrmecochory
2	Leaf dry matter content (LDMC) 99 (95%)	1	mg.g ⁻¹
3	Plant height (Height) 99 (100%)	1	Maximum vegetative height (m)
4	Plant life-form 99 (100%)	2	Geophyte; hemicryptophyte, liana-phanerophyte and phanerophyte
5	Plant life-span 99 (100%)	1	Perennial and short-lived
6	Seed dry mass 89 /99 (89%)	1	mg
7	Pollination 99 (100%)	2	Anemogamy; autogamy; entomogamy; hydrogamy
8	Specific leaf area (SLA) 99 (100%)	1	mm ² .g ⁻¹
9	Flowering phenology 99 (100%)	3	Start of flowering: months (1-12)

587

588

589

590

591

592 **Table S3.** Description of functional traits used to characterize spider species, from the literature.

Functional traits	Description and units	Reference
Body size	Categorical (3) Small (<9 mm); Medium (9-15mm); Large (> 15mm)	Roberts (1995)
Guilds	Categorical (7) Ambush hunters, Ground hunters, Others hunters, Sheet web, Space web, Orb web, Wandering web	Cardoso et al., (2011)
Phenology	Categorical (4) Spring, Summer, Autumn-Winter, Eurychron	Harvey et al., (2002)
Circadian activity	Categorical (3) Diurnal, Nocturnal, Both	Cardoso et al., (2011)

593

594 Buchar, J. & Ruzicka, V. (2002) *Catalogue of Spiders of the Czech Republic*.

595 Cardoso, P., Pekár, S., Jocqué, R. & Coddington, J.A. (2011) Global Patterns of Guild Composition and
596 Functional Diversity of Spiders (ed M Somers). *PLoS ONE*, 6, e21710.

597 Harvey, P.R., Nellist, D.R. & Telfer, M.G. (2002) *Provisional Atlas of British Spiders (Arachnida,*
598 *Araneae)*, Biological Records Center. Huntington, UK.

599 Roberts, M.J. (1995) *Spiders of Britain & Northern Europe*. Harper Collins, London; New York.

600

601

602

603

604

605

606

607

608

609 **Table S4.** Description of functional entities (FE) identified for spiders.

# FE	Functional entities	Body	Phenology	Circadian activity	Hunting	n species
1	Bla_Peu_Dbo_Hgr	Large	Eurychron	Both	Ground_hunters	3
2	Bsm_Psu_Dbo_Hsh	Small	Summer	Both	Sheetweb	1
3	Bla_Psu_Ddi_Hgr	Large	Summer	Diurnal	Ground_hunters	6
4	Bme_Peu_Dbo_Hgr	Medium	Eurychron	Both	Ground_hunters	2
5	Bla_Peu_Dbo_Ham	Large	Eurychron	Both	Ambush_hunters	1
6	Bsm_Peu_Dbo_Hsh	Small	Eurychron	Both	Sheetweb	10
7	Bsm_Pau_Dbo_Hsh	Small	Autumn-Winter	Both	Sheetweb	4
8	Bme_Peu_Dbo_Hsh	Medium	Eurychron	Both	Sheetweb	6
9	Bsm_Psu_Dbo_Hwa	Small	Summer	Both	Wandering_web	4
10	Bla_Psu_Dno_Hot	Large	Summer	Nocturnal	Otherhunters	1
11	Bla_Peu_Dno_Hot	Large	Eurychron	Nocturnal	Otherhunters	1
12	Bla_Psp_Dno_Hsh	Large	Spring	Nocturnal	Sheetweb	1
13	Bsm_Peu_Dbo_Hwa	Small	Eurychron	Both	Wandering_web	15
14	Bla_Psp_Dbo_Hgr	Large	Spring	Both	Ground_hunters	1
15	Bla_Peu_Dno_Hgr	Large	Eurychron	Nocturnal	Ground_hunters	1
16	Bme_Peu_Dbo_Hsp	Medium	Eurychron	Both	Spaceweb	2
17	Bla_Pau_Dbo_Hsh	Large	Autumn-Winter	Both	Sheetweb	1
18	Bme_Peu_Dbo_Hwa	Medium	Eurychron	Both	Wandering_web	5
19	Bme_Psu_Dbo_Hwa	Medium	Summer	Both	Wandering_web	1
20	Bla_Psu_Dbo_Hgr	Large	Summer	Both	Ground_hunters	3
21	Bla_Psp_Ddi_Hgr	Large	Spring	Diurnal	Ground_hunters	1
22	Bla_Peu_Dbo_Hsh	Large	Eurychron	Both	Sheetweb	1
23	Bme_Psp_Dbo_Hsh	Medium	Spring	Both	Sheetweb	1
24	Bla_Psu_Dbo_Hor	Large	Summer	Both	Orbweb	1
25	Bsm_Peu_Ddi_Hot	Small	Eurychron	Diurnal	Otherhunters	1
26	Bme_Peu_Dbo_Ham	Medium	Eurychron	Both	Ambush_hunters	2
27	Bla_Peu_Dbo_Hor	Large	Eurychron	Both	Orbweb	1
28	Bme_Peu_Dbo_Hor	Medium	Eurychron	Both	Orbweb	1
29	Bla_Peu_Ddi_Hgr	Large	Eurychron	Diurnal	Ground_hunters	3
30	Bsm_Psu_Dbo_Hgr	Small	Summer	Both	Ground_hunters	1
31	Bsm_Psp_Dbo_Hwa	Small	Spring	Both	Wandering_web	2
32	Bsm_Pau_Dbo_Hwa	Small	Autumn-Winter	Both	Wandering_web	1
33	Bsm_Psu_Dbo_Hsp	Small	Summer	Both	Spaceweb	1
34	Bme_Psp_Dbo_Hwa	Medium	Spring	Both	Wandering_web	1
35	Bla_Psu_Dbo_Ham	Large	Summer	Both	Ambush_hunters	2

610

611

612

613

614

615 **Table S5.** Occurrence frequency (%) in ancient and recent forests of observed diversity of (i)
 616 functional groups of plants (in bold) and plant species and (ii) functional entities of spiders (in bold)
 617 and spider species. The average observed diversity per plot is also given, that is, the average richness
 618 per plot in terms of species and functional groups and entities. See Table S4 and Figure S1 for
 619 description of functional groups end entities.

PLANTS			
FG/FE	Species	Ancient forests	Recent woodlands
FG #1 Spring	perennials herbs	0,55	0,92
	<i>Euphorbia amygdaloides</i>	0,15	0,67
	<i>Heracleum sphondylium</i>	0,00	0,08
	<i>Lamium galeobdolon</i>	0,05	0,00
	<i>Ranunculus repens</i>	0,00	0,08
	<i>Scrophularia nodosa</i>	0,00	0,08
	<i>Stachys officinalis</i>	0,00	0,08
	<i>Stachys sylvatica</i>	0,00	0,33
	<i>Stellaria holostea</i>	0,45	0,25
	<i>Teucrium scorodonia</i>	0,15	0,17
	<i>Veronica chamaedrys</i>	0,00	0,17
	<i>Vinca minor</i>	0,05	0,00
	<i>Viola reichenbachiana</i>	0,10	0,42
FG #2 Small, mid-spring	flowering herbs	0,25	0,75
	<i>Ajuga reptans</i>	0,05	0,58
	<i>Geum urbanum</i>	0,00	0,75
	<i>Hypericum pulchrum</i>	0,25	0,00
	<i>Lysimachia nemorum</i>	0,05	0,00
	<i>Potentilla sterilis</i>	0,00	0,17
FG #3 Vernal	geophytes	0,50	1,00
	<i>Anemone nemorosa</i>	0,10	0,08
	<i>Circaea lutetiana</i>	0,00	0,67
	<i>Conopodium majus</i>	0,05	0,17
	<i>Hyacinthoides non-scripta</i>	0,20	0,08
	<i>Listera ovata</i>	0,00	0,33
	<i>Mercurialis perennis</i>	0,00	0,17
	<i>Polygonatum multiflorum</i>	0,35	0,33
	<i>Tamus communis</i>	0,05	0,42
FG #4 Short-lived	herbs	0,35	0,75
	<i>Cardamine flexuosa</i>	0,00	0,08
	<i>Digitalis purpurea</i>	0,05	0,08
	<i>Galeopsis tetrahit</i>	0,00	0,08
	<i>Galium aparine</i>	0,00	0,58
	<i>Geranium robertianum</i>	0,00	0,58
	<i>Moehringia trinervia</i>	0,00	0,25
	<i>Oxalis acetosella</i>	0,30	0,00

FG #5 Ferns	1,00	1,00
<i>Athyrium filix.femina</i>	0,20	0,42
<i>Blechnum spicant</i>	0,50	0,00
<i>Dryopteris affinis</i>	0,00	0,50
<i>Dryopteris carthusiana</i>	0,15	0,08
<i>Dryopteris dilatata</i>	0,25	0,58
<i>Dryopteris filix-mas</i>	0,00	0,83
<i>Polypodium vulgare</i>	0,35	0,08
<i>Polystichum setiferum</i>	0,00	0,50
<i>Pteridium aquilinum</i>	1,00	0,67
FG #6 Tall, summer flowering herbs	0,95	0,92
<i>Agrostis capillaris</i>	0,25	0,00
<i>Agrostis curtisii</i>	0,05	0,00
<i>Arrhenatherum elatius</i>	0,10	0,00
<i>Brachypodium sylvaticum</i>	0,10	0,67
<i>Carex laevigata</i>	0,05	0,00
<i>Carex pallescens</i>	0,05	0,00
<i>Carex pendula</i>	0,05	0,00
<i>Carex pilulifera</i>	0,55	0,08
<i>Carex remota</i>	0,00	0,50
<i>Carex sylvatica</i>	0,15	0,08
<i>Dactylis glomerata</i>	0,10	0,00
<i>Deschampsia cespitosa</i>	0,10	0,00
<i>Holcus lanatus</i>	0,00	0,17
<i>Holcus mollis</i>	0,60	0,17
<i>Juncus effusus</i>	0,10	0,08
<i>Luzula sylvatica</i>	0,15	0,00
<i>Luzula multiflora</i>	0,05	0,00
<i>Melica uniflora</i>	0,10	0,00
<i>Milium effusum</i>	0,35	0,00
<i>Molinia caerulea</i>	0,30	0,00
<i>Rumex acetosa</i>	0,00	0,08
<i>Rumex conglomeratus</i>	0,00	0,08
<i>Rumex sanguineus</i>	0,00	0,58
<i>Urtica dioica</i>	0,00	0,42
FG #7 Mesophanerophytes	0,50	1,00
<i>Betula pendula</i>	0,15	0,00
<i>Carpinus betulus</i>	0,15	0,50
<i>Corylus avellana</i>	0,35	0,67
<i>Fraxinus excelsior</i>	0,00	0,83
<i>Frangula alnus</i>	0,15	0,00
<i>Populus tremula</i>	0,10	0,08
<i>Taxus baccata</i>	0,05	0,00
<i>Tilia cordata</i>	0,05	0,00
FG #8 Megaphanerophytes	0,95	0,67
<i>Castanea sativa</i>	0,45	0,25

	<i>Fagus sylvatica</i>	0,70	0,17
	<i>Quercus petraea</i>	0,50	0,00
	<i>Quercus rubra</i>	0,05	0,08
	<i>Quercus robur</i>	0,30	0,58
FG #9 Schrubbs		1,00	1,00
	<i>Calluna vulgaris</i>	0,05	0,00
	<i>Cornus sanguinea</i>	0,00	0,42
	<i>Crataegus monogyna</i>	0,10	0,58
	<i>Cytisus scoparius</i>	0,15	0,08
	<i>Euonymus europaeus</i>	0,00	0,58
	<i>Hedera helix</i>	0,95	1,00
	<i>Ilex aquifolium</i>	0,90	0,58
	<i>Malus communis</i>	0,05	0,00
	<i>Prunus avium</i>	0,05	0,17
	<i>Prunus laurocerasus</i>	0,10	0,00
	<i>Prunus spinosa</i>	0,10	0,50
	<i>Pyrus pyraster</i>	0,20	0,00
	<i>Ribes rubrum</i>	0,00	0,17
	<i>Ruscus aculeatus</i>	0,20	0,17
	<i>Sambucus nigra</i>	0,00	0,33
	<i>Sorbus aucuparia</i>	0,20	0,00
	<i>Viburnum opulus</i>	0,00	0,08
FG #10 Nanophanerophytes		1,00	1,00
	<i>Lonicera periclymenum</i>	0,85	0,83
	<i>Rosa arvensis</i>	0,05	0,08
	<i>Rubus fruticosus</i>	1,00	1,00
	<i>Vaccinium myrtillus</i>	0,35	0,00
TOTAL			
	<i>Mean FG richness ± se</i>	7.0 ± 1.7	9.2 ± 1.2 *
	<i>Mean species richness ± se</i>	16.4 ± 7.0	24.1 ± 8.1 **

SPIDERS

1-Large ground-hunters eurychron both		0,2	0,50
	<i>Agroeca brunnea</i>	0,05	0,42
	<i>Cicurina cicur</i>	0,05	0,08
	<i>Zora spinimana</i>	0,1	0,00
2-Small sheetweb summer both		0,2	0,58
	<i>Agyneta ramosa</i>	0,2	0,58
3-Large ground-hunters summer diurnal		0,75	0,75
	<i>Alopecosa pulverulenta</i>	0,15	0,00
	<i>Pardosa hortensis</i>	0,1	0,00
	<i>Pardosa prativaga</i>	0,05	0,00
	<i>Pardosa saltans</i>	0,75	0,75
	<i>Pirata uliginosus</i>	0,1	0,00

<i>Piratula hygrophila</i>	0,2	0,00
4-Medium ground-hunters eurychron both	0,35	0,00
<i>Apostenus fuscus</i>	0,25	0,00
<i>Scotina celans</i>	0,1	0,00
5-Large ambush-hunters eurychron both	0,05	0,00
<i>Atypus affinis</i>	0,05	0,00
6-Small sheetweb eurychron both	1	1,00
<i>Bathyphantes gracilis</i>	0,05	0,08
<i>Centromerus dilutus</i>	0,35	0,25
<i>Centromerus serratus</i>	0,15	0,08
<i>Diplostyla concolor</i>	0,1	0,83
<i>Hahnia helveola</i>	0,2	0,00
<i>Iberina montana</i>	0,05	0,00
<i>Maro minutus</i>	0,1	0,00
<i>Microneta viaria</i>	1	1,00
<i>Palliduphantes pallidus</i>	0,8	0,67
<i>Tenuiphantes flavipes</i>	0,25	0,75
7-Small sheetweb autumn-winter both	0,8	0,67
<i>Centromerus brevipalpus</i>	0,8	0,58
<i>Hahnia ononidum</i>	0,05	0,00
<i>Saloca diceros</i>	0,05	0,00
<i>Tenuiphantes cristatus</i>	0	0,25
8-Medium sheetweb eurychron both	1	1,00
<i>Centromerus sylvaticus</i>	0,25	0,25
<i>Macrargus rufus</i>	0,9	0,33
<i>Neriene clathrata</i>	0,1	0,00
<i>Saaristoa abnormis</i>	0,7	0,67
<i>Tenuiphantes tenuis</i>	0,15	0,25
<i>Tenuiphantes zimmermanni</i>	1	1,00
9-Small wandering-web summer both	0,75	0,75
<i>Ceratinella scabrosa</i>	0,3	0,67
<i>Diplocephalus picinus</i>	0,55	0,42
<i>Gongylidiellum latebricola</i>	0,1	0,00
<i>Walckenaeria atrotibialis</i>	0,05	0,25
10-Large otherhunters summer nocturnal	0,25	0,08
<i>Clubiona comta</i>	0,25	0,08
11-Large otherhunters eurychron nocturnal	0,15	0,08
<i>Clubiona terrestris</i>	0,15	0,08
12-Large sheetweb spring nocturnal	0,4	0,08
<i>Coelotes terrestris</i>	0,4	0,08
13-Small wandering-web eurychron both	1	1,00
<i>Dicymbium tibiale</i>	0,1	0,33
<i>Diplocephalus latifrons</i>	0	0,58
<i>Erigone atra</i>	0,05	0,00
<i>Gongylidiellum vivum</i>	0,05	0,00
<i>Jacksonella falconeri</i>	0,05	0,00

<i>Micrargus apertus</i>	0,45	0,17
<i>Micrargus herbigradus</i>	0,1	0,50
<i>Monocephalus fuscipes</i>	0,75	0,83
<i>Ostearius melanopygius</i>	0	0,25
<i>Parapelecopsis nemoralis</i>	0,05	0,00
<i>Sintula corniger</i>	0	0,08
<i>Walckenaeria cucullata</i>	0,7	0,00
<i>Walckenaeria cuspidata</i>	0,45	0,00
<i>Walckenaeria nudipalpis</i>	0	0,08
<i>Wiehlea calcarifera</i>	0,05	0,00
14-Large ground-hunters spring both	0	0,08
<i>Drassyllus lutetianus</i>	0	0,08
15-Large ground-hunters eurychron nocturnal	0,65	0,33
<i>Dysdera erythrina</i>	0,65	0,33
16-Medium spaceweb eurychron both	0,5	0,75
<i>Enoplognatha thoracica</i>	0,05	0,00
<i>Robertus lividus</i>	0,5	0,75
17-Large sheetweb autumn-winter both	0,55	0,00
<i>Eratigena picta</i>	0,55	0,00
18-Medium wandering-web eurychron both	0,75	0,33
<i>Gonatium rubellum</i>	0,1	0,00
<i>Oedothorax apicatus</i>	0	0,08
<i>Walckenaeria acuminata</i>	0,5	0,25
<i>Walckenaeria incisa</i>	0,05	0,08
<i>Walckenaeria obtusa</i>	0,55	0,08
19-Medium wandering-web summer both	0,05	0,00
<i>Gonylidium rufipes</i>	0,05	0,00
20-Large ground-hunters summer both	0,25	0,08
<i>Haplodrassus silvestris</i>	0,2	0,00
<i>Trachyzelotes pedestris</i>	0,05	0,00
<i>Zelotes apricorum</i>	0,05	0,08
21-Large ground-hunters spring diurnal	0,05	0,00
<i>Hygrolycosa rubrofasciata</i>	0,05	0,00
22-Large sheetweb eurychron both	0,05	0,00
<i>Labulla thoracica</i>	0,05	0,00
23-Medium sheetweb spring both	0	0,08
<i>Linyphia hortensis</i>	0	0,08
24-Large orbweb summer both	0,1	0,08
<i>Metellina mengei</i>	0,1	0,08
25-Small otherhunters eurychron diurnal	0,05	0,00
<i>Neon reticulatus</i>	0,05	0,00
26-Medium ambush-hunters eurychron both	0,15	0,33
<i>Ozyptila praticola</i>	0,05	0,08
<i>Ozyptila trux</i>	0,1	0,33
27-Large orbweb eurychron both	0	0,08
<i>Pachygnatha clercki</i>	0	0,08

28-Medium orbweb eurychron both	0,05	0,00
<i>Pachygnatha degeeri</i>	0,05	0,00
29-Large ground-hunters eurychron diurnal	0,6	0,50
<i>Pardosa pullata</i>	0,1	0,00
<i>Trochosa ruricola</i>	0,05	0,00
<i>Trochosa terricola</i>	0,5	0,50
30-Small ground-hunters summer both	0,05	0,00
<i>Phrurolithus festivus</i>	0,05	0,00
31-Small wandering-web spring both	0,1	0,08
<i>Pocadicnemis pumila</i>	0,05	0,00
<i>Walckenaeria dysderoides</i>	0,05	0,08
32-Small wandering-web autumn-winter both	0,15	0,00
<i>Tapinocyba mitis</i>	0,15	0,00
33-Small spaceweb summer both	0	0,33
<i>Theridion mystaceum</i>	0	0,33
34-Medium wandering-web spring both	0,15	0,08
<i>Walckenaeria mitrata</i>	0,15	0,08
35-Large ambush-hunters summer both	0,1	0,00
<i>Xysticus cristatus</i>	0,05	0,00
<i>Xysticus luctator</i>	0,05	0,00
TOTAL		
<i>Mean FE richness ± se</i>	11.3 ± 2.9	9.7 ± 1.7
<i>Mean species richness ± se</i>	18.8 ± 6.0	16.6 ± 3.3

620

621

622

623

624

625

626

627

628

629

630

631

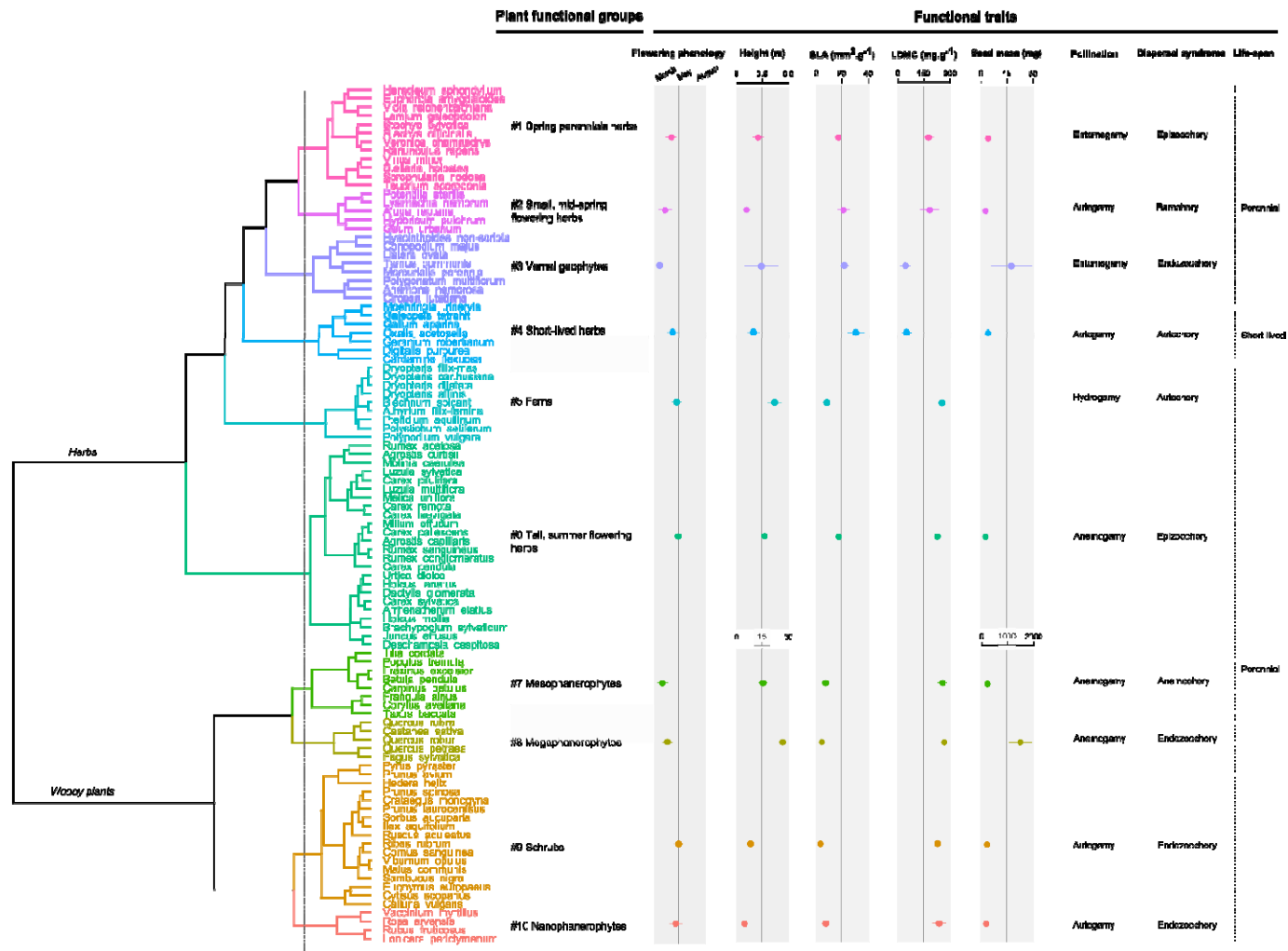


Figure S1. Functional groups of plant species identified with the dendrogram method (see Materials and Methods for more details). For each functional group, the mean of continuous traits and the dominant modality of categorical traits are given.

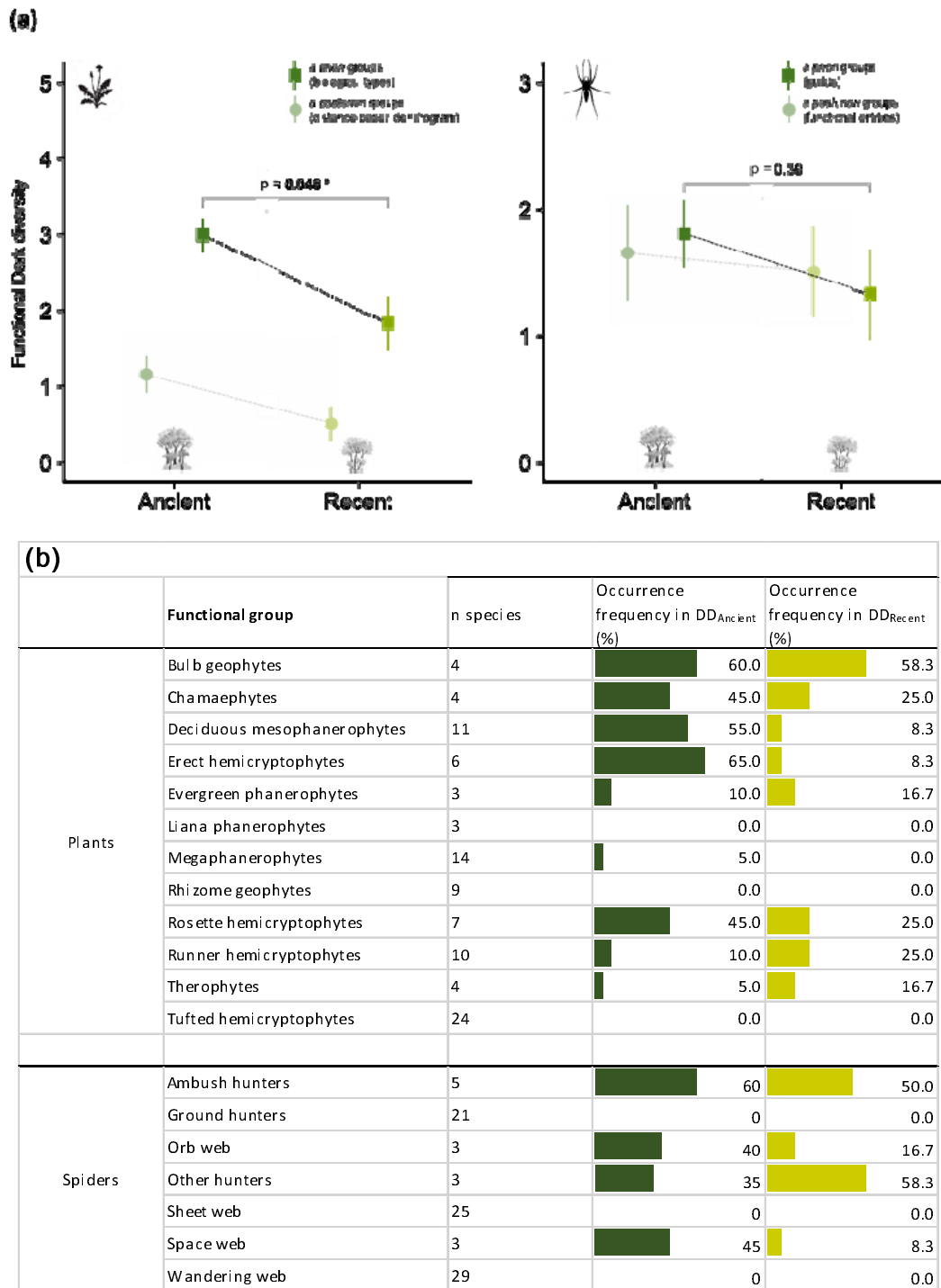


Figure S2. Comparisons between ancient and recent forests of (a) functional dark diversity and (b) its composition, based on functional groups defined *a priori* (Julve's groups for plants and Cardoso's guilds for spiders). Results are very similar to those obtained with groups defined *a posteriori* (Figure 4 and in light grey here): functional dark diversity is higher in ancient forests for plant communities (and with a different composition), and functional dark diversity is equivalent between both forest types for spiders (with also a different composition).