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Journal of Applied Ecology

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

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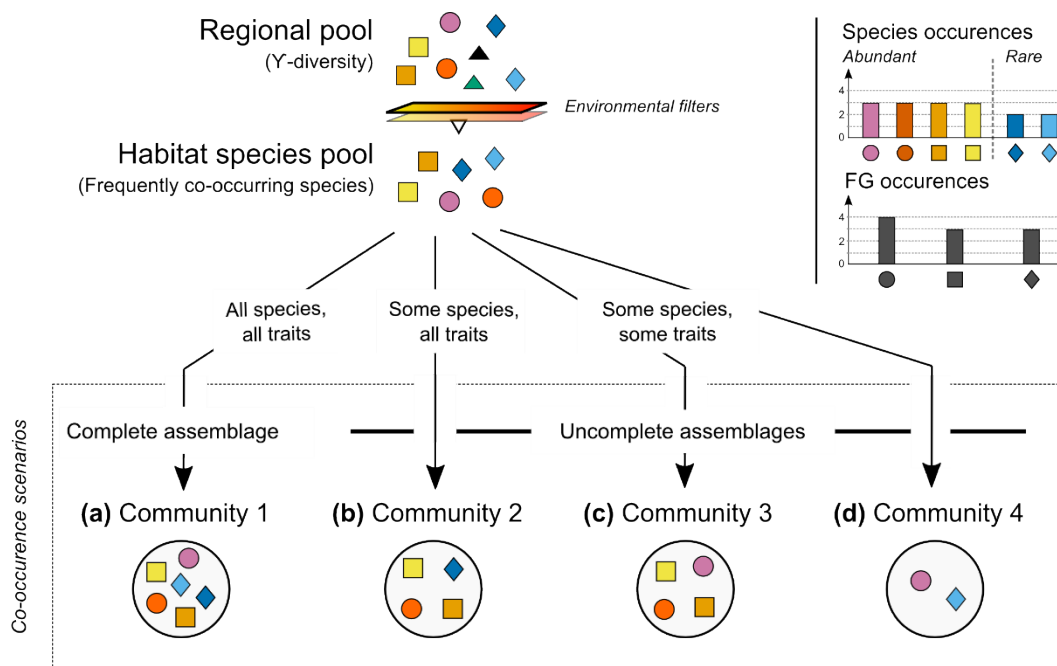
Abstract

1. The conservation of natural habitats requires an accurate assessment of both their degradation and their potential for restoration. Among the tools available, dark diversity is promising, since it estimates all the species that could be present in a community due to favourable environmental conditions but are currently lacking. However, current experimental approaches measure dark diversity mainly from species co-occurrences, which rely partly on neutral processes, and also suffer from several problems concerning the inclusion of rare species.
2. Here, we propose a novel method to estimate dark diversity, which is based on more deterministic co-occurrence and also strongly limits the problems of rarity: the co-occurrence of species' functional features. We adapted the Beals' co-occurrence index using functional groups, and we estimated functional dark diversity based on co-occurrence of functional groups. To illustrate the interests of our approach, we then addressed as an example a major issue of restoration ecology: how does passive rewilding (i.e. spontaneous restoration of woodlands) impact the ecological integrity of recovered communities? We compared post-agricultural woodlands with ancient forests, in terms of taxonomic and functional dark diversity of vascular plants and spiders.
3. For both taxa, the patterns of dark diversity in recent woodlands and ancient forests changed depending on whether we used the taxonomic or functional approach. This was due to the detection of functional features even if they were hosted by rare species, and to the consideration of ecological redundancy between species in functional groups. Notably, recent woodlands harboured plant communities with a similar amount of taxonomic dark diversity compared to ancient forests, but with less functional dark diversity. Also, the composition of functional dark diversity clearly differed between forest types.
4. *Synthesis and applications.* Functional dark diversity brings novel perspectives for ecological diagnostic and restoration. In particular, it provides a more mechanistic understanding of the constraints which limit the re-assembly of natural communities during restoration practices (e.g. dispersal limitation). The functional approach usefully complements the taxonomical one to identify habitat conservation and restoration interests, especially for highly degraded sites where the detection of missing groups via species is biased because of their rarity.

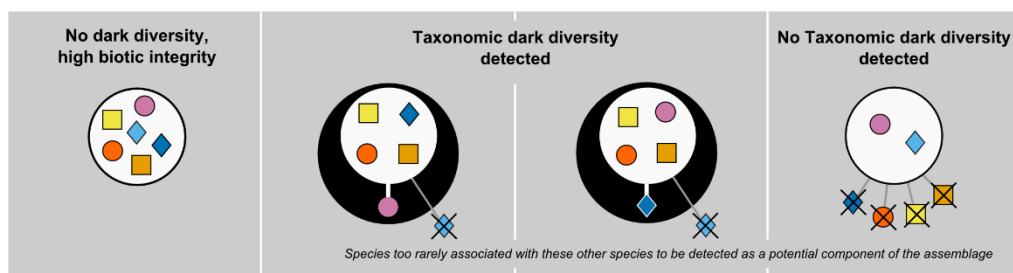
Keywords: community assembly, ecological restoration, forest temporal continuity, passive rewilding, plants, spiders, taxonomic and functional dark diversity

Introduction

The increasing degradation of natural habitats calls for effective conservation and restoration actions. Conservation can be prioritised among sites and habitats of interest, and management strategies can be adapted to the local context, but all of this requires an accurate and complete assessment of the potential of communities to be restored. The concept of *dark diversity* has been introduced in Ecology by Pärtel et al., (2011), to consider the potential biodiversity of natural communities. In a given community, the dark diversity represents the diversity of species that are locally absent while they are present in the regional pool and could be present due to favourable environmental conditions. Precisely, dark diversity identifies species that are absent due to dispersal limitation or historical contingencies, but not species that are absent due to recruitment limitation (that should be absent anyway) nor species that the sampling failed to observe (dormant or very rare species, see Pärtel, 2014). Dark diversity places biodiversity into a dynamic perspective: for example, it integrates species with a colonisation credit, which are species likely to be recruited in the future due to favourable environmental conditions or delayed population growth (Jackson & Sax, 2010). By studying the differences between observed and dark biodiversity we can also easily investigate the assembly processes without resorting to complex statistical analyses or integration of multiple environmental variables, which is very useful from an applied ecology perspective (Pärtel, 2014; Pärtel et al., 2011). Among the three main high-level processes that structure communities at local scales, namely dispersal, ecological drift and niche selection (Vellend, 2016), the use of dark diversity makes it possible to distinguish the relative part of dispersal and niche selection (also called recruitment) in the structuring of communities: species absent in both observed and dark diversity are limited by recruitment, and species absent in observed diversity but present in dark diversity are limited by their dispersal capacities as well potential ecological drift (e.g. a species may miss because another one, functionally close, already occupy the niche). Therefore, dark diversity brings information that neither the structure nor the composition alone of observed diversity can bring. Moreover, identifying the dark diversity of communities enables to guide the conservation efforts and the restoration strategies, since it helps to determine the taxa that are frequently absent (e.g. see Moeslund et al., 2017), the habitats more or less degraded, their restoration potential and success (Noreika et al., 2020), and, conversely, the habitats that are the most complete (i.e. with the lowest dark diversity, Lewis et al., 2017) and that could hence be priority targets for conservation. However, to date, the studies evaluating dark diversity and species pools are mainly restricted to the taxonomic facet of communities, hence to species' identities (Spasojevic et al., 2018).



Taxonomic dark diversity



Functional dark diversity

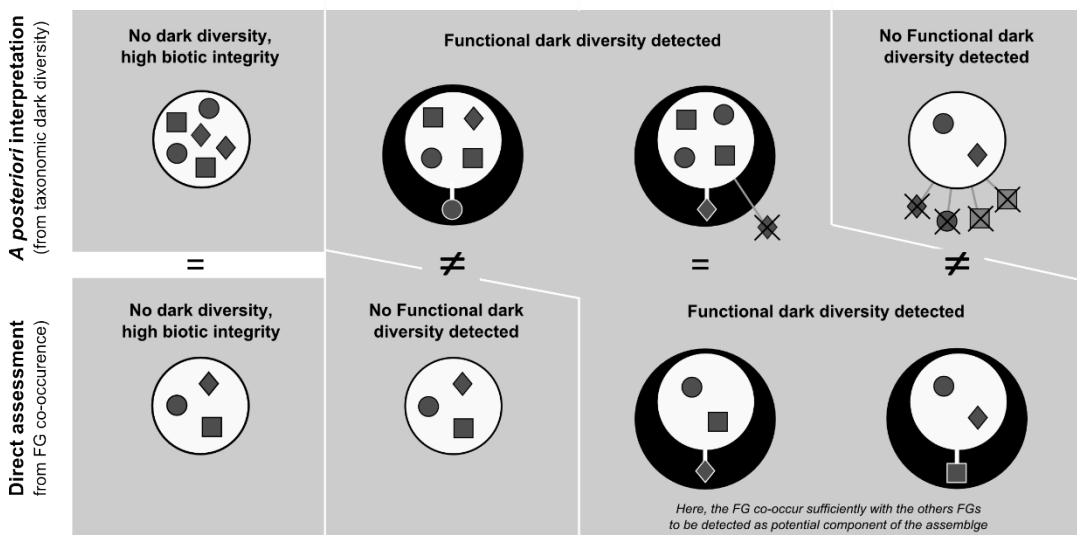


Figure 1. Four distinct co-occurrence scenarios in several communities (a, b, c, d) from a single habitat-specific species pool. The colour of a drawing represent a species identity, and its shape represent its

functional group. From these local co-occurrences taken together, taxonomic dark diversity and functional dark diversity (represented by black circles) can be estimated for the four communities. Functional dark diversity estimated *a posteriori* (i.e. functional interpretation of taxonomic dark diversity) mirrors taxonomic dark diversity, because it is only the translation into traits of the species which are lacking. Functional dark diversity estimated *a priori* from the co-occurrence of functional groups differs from taxonomic dark diversity and hence from functional dark diversity estimated *a posteriori*. In particular, in the second community (b), a species is lacking, so its functional group seems also lacking. However, this functional group is in fact already present in the community and, provided that the functional traits fully represent the niche dimensions, the probability of recruitment of another species of its functional group is considerably reduced because the niche is already occupied. In the fourth community (d), many species are lacking but their co-occurrences with the present species are too rare, so these species are not integrated into the taxonomic dark diversity. However, the co-occurrence of their functional groups is frequent, thus the lacking functional group, despite hosted by rare species, is integrated into the functional dark diversity calculated *a priori*. Note that in the case (b), niche overlapping can be considered *a posteriori* so functional groups present both in the dark diversity and in the observed diversity can be removed from dark diversity, which will then give the same results than our method, but indirectly; however, in the case (d), no manipulation of functional dark diversity calculated *a posteriori* is able to retrieve rare species, so the results must be different between *a posteriori* and *a priori* approaches. Also note that our method does not permit to catch rare functional groups, but the rarity of functional groups is itself rare and always less frequent than that of species.

Incorporating functional traits of species into direct assessments of dark diversity could bring many novel insights. Functional traits are all the features of species that can either respond to environmental conditions or can impact ecosystem functions, or both (Violle et al., 2007). Basically, these are morphological, physiological or phenological features, for example the life form of a plant or the type of diet of an animal. The tools that are currently available for measuring directly dark diversity do not consider functional traits, overlooking the ecological differences that may exist between or within taxa. Functional traits can be very different among taxa but also within taxa (Prinzing et al., 2008), and in taxa occupying particular environments (Hermant et al., 2012). Alternatively, at some trophic level, several species can have similar functional traits and can therefore be redundant in the impact they have on ecosystem functions or in the response they have to disturbances or environmental changes. Consequently, a given taxonomic dark diversity could or could not represent a functional dark diversity

(Figure 1b, c, d), which would bring very different information about the interest in conservation and the capacity of communities to be ecologically restored.

While a functional interpretation of taxonomic dark diversity can be made *a posteriori* (i.e. *what are the traits of the species which are absent* ? e.g. see Belinchón et al., 2020), we think that the calculation of taxonomic dark diversity, which is based in most cases on co-occurrence of species (Lewis et al., 2016), can in itself limit the detection of functional patterns. Variations of taxonomic diversity have been shown to sometimes result from non-deterministic processes such as neutral coexistence (i.e. ecological drift, Chase & Leibold, 2003), suggesting that taxonomic diversity could be a somewhat unreliable and unpredictable parameter, also influenced by stochastic processes. Moreover, taxonomic dark diversity taken alone can potentially underestimate the ecological integrity of a community (i.e. the capacity of a community to harbour community structure similar to those of undisturbed ecosystems in the region) because it does not consider the functional redundancy within taxa and the niche filling within habitats (Figure 1b). Most importantly, modern ecology has shown that the coexistence of functional features, which can be traits or combinations of traits, is much more informative about the processes involved in communities assembly than the only coexistence of species (McGill et al., 2006). What coexist are functional features, much more than truly independent species: for plants, for example chamephytes, therophytes and small hemicryptophytes in peatlands, helophytes and hydrophytes in marshes, woody species, shrubs, lianas and small herbs in forests... Consequently, accounting for functional features in the co-occurrence calculation becomes a necessity if we want to correctly infer from the concept of dark diversity the deterministic processes of community assembly and identify the potential functions that can realistically be provided in natural communities; and thus, take fully appropriate conservation and restoration policies. Last, an assessment of functional dark diversity through co-occurrence of functional features would also increase the probability of detecting functional features hosted by rare species: the co-occurrences of these species might be too rare for them to be included in the taxonomic dark diversity (so their groups would not be included either with an *a posteriori* interpretation), but the co-occurrences of their groups may be sufficiently frequent for the groups to be included in the functional dark diversity (Figure 1d).

Terrestrial ecosystems currently experience many land-use changes, which raises important questions about their impacts on biodiversity and natural habitats (Newbold et al., 2015). In particular, how communities of ancient forests (i.e. uninterrupted forests since several centuries, Hermy et al., 1999) differ from those of recent woodlands (appeared spontaneously following land abandonment) is an old but persistent issue of ecology (Bergès & Dupouey, 2020), which offers an ideal opportunity to make use

of dark diversity. Indeed, the interruption of forest temporal continuity generally induces two major constraints for the forest re-assembly: recruitment limitation and dispersal limitation, respectively due to past land-uses (e.g. fertilisation or soil disturbance) and spatio-temporal fragmentation of source habitats (Bergès & Dupouey, 2020; Hermy & Verheyen, 2007). Through historical contingencies, the spontaneous recovering of communities after interruption of forest temporal continuity also involves the ecological drift. Consequently, the composition and structure of communities in recent woodlands often differ strongly from those of ancient forests. Notably, recent woodlands often lack specialised, typical plant species of ancient forests, which are characterised by low seed production, low dispersal capacities, and require very precise ecological conditions such as oligotrophic substrates and soils weakly disturbed (Hermy & Verheyen, 2007). On the other hand, the reduction of soil nutrient limitations and the environmental heterogenization due to past land-uses can lead to the recruitment of more diverse functional features in recent woodlands (Morel et al., 2019b), thus increasing the levels of both observed and potential (dark) alpha diversity. Animal groups may also be sensitive to the forest temporal continuity, in particular arthropods, which are highly dependent to local habitat conditions (Hofmeister et al., 2019). Among arthropods, spiders might be particularly interesting to survey because they are ubiquitous in all terrestrial ecosystems, and the structure of their community might be gradually reshaped during the successional trajectory (Morel et al., 2019a). Overall, many aspects of the ecological consequences of the rupture of forest temporal continuity remain to be explored more in depth, for instance the relative importance of dispersal limitation, recruitment limitation and ecological drift on biodiversity recovering, which is highly context-dependant (see Bergès & Dupouey, 2020). Thus, the application of the dark diversity framework should enable to obtain a more realistic vision of the capacities of ecosystems to spontaneously recover biodiversity.

Here, we developed the first method to directly estimate functional dark diversity, and we applied this method to evaluate how passive rewilding (i.e. spontaneous afforestation) may reshape the biocenosis of forest ecosystems. We sampled plant and spider communities, two main understorey taxa which depend on distinct biotic and abiotic conditions, and characterised their spectrum of functional traits. We calculated taxonomic dark diversity using the species co-occurrence method (Lewis et al., 2016) and adapted this method to assess functional dark diversity, using co-occurrence of functional groups, which were identified through multitrait differences. To explore the methodological improvements of our method, we also assessed functional dark diversity indirectly (i.e. *a posteriori*), from taxonomic dark diversity. Then, we compared recent woodlands with ancient forests for taxonomic and dark diversity. We tested the following hypotheses: (i) functional dark diversity assessed directly does not equate to

taxonomic dark diversity or to functional dark diversity assessed indirectly, (ii) the composition of functional dark diversity is specific to the forest type, illustrating their different ecological constraints (e.g. the relative role of dispersal limitation), (iii) recent woodlands harbour plant and spider communities with both higher taxonomic and functional dark diversity than ancient forests (i.e. restoration is partially effective).

Materials and methods

Study sites

We conducted the study in different forest environments of Western Europe (Brittany, France). We selected 32 plots of mesophilic, oak and beech-dominated mature forests, within sites sharing similar geological substrates (mainly granite rocks and schists), thereby strongly limiting the influence of environmental heterogeneity and stand maturity. These plots were homogeneous management units of around 1 ha and were distributed across 8 sites (ranging from 200 to 4000 ha) within the regional area. We set apart plots of ancient forests from those of recent woodlands by checking the temporal forest continuity thanks to the historical Cassini map layers (year 1790) and the Napoleonic cadastre (year 1847), that is, the two reference documents in France for the historical land-uses (Cateau et al., 2015). We defined ancient forests as sites already forested in the middle of the 18th century (when the overall forested area was at its minimum over the French territory, Cateau et al., 2015) and recent woodlands as forests resulting from farmland abandonment during the 20th century. Therefore, ancient forests have an uninterrupted forest state since at least 230 years and recent woodlands are not older than 120 years. Our dataset included 20 plots in ancient forests (from six different forest sites) and 12 plots in recent woodlands (from two different forest sites); see Figure S1. The site configuration, the habitat structure and the ecological conditions were quite similar between recent and ancient forests: there were no differences of site area, canopy cover, basal area and Ellenberg Indicator Values (EIV) for moisture degree (Table S1). But, EIV showed higher pH and nutrient concentration and lower affinity for light in recent woodlands in comparison to ancient forests (i.e. there were more shade-loving species in recent woodlands, Table S1), which is consistent with previous studies investigating environmental conditions in post-agricultural woodlands (Koerner et al., 1997). Plots were at least 100 m away from the nearest forest edge to minimize edge effects.

Community sampling

We conducted floristic surveys in June-July 2014 and 2015 to sample the understorey plant communities of the selected plots (i.e. below 2 meters high and including woody species). We used 50-m² quadrats (10 x 5 m) and we noted all species encountered belonging to the herbaceous and shrub strata. A total of 99 species was recorded (see Morel et al., 2019b for more details on the dataset).

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

Functional characterisation of species

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

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

Identification of functional groups

Since we aimed at using a co-occurrence index to calculate functional dark diversity, we needed to divide the species pool into discontinuous elements, that is, functional groups. For plants, we divided the species pool into functional groups following the methods of Verheyen et al. (2003), which were used in a similar investigation of recent versus ancient understorey plant communities. This method allows to identify functional groups according to trait correlations and thus select objectively consistent ecological groups. First, we calculated a species-to-species distance matrix with the Gower's similarity coefficient since this coefficient can deal with missing values and both quantitative and qualitative data. Then, we used this matrix to cluster the species into functional groups using the Ward's method (Murtagh & Legendre, 2014). The number of groups was determined graphically from visual screening of the dendrogram after searching the optimal number of clusters by assessing the average silhouette of observations for different values of k clusters (see Figure S2). We identified 10 functional groups of plant species for which functional variation was minimized within groups and maximized between groups: 4 groups of woody plants and 6 groups of herbaceous and graminoid species (Figure S3). We made sure that the selected groups were ecologically relevant, that is, corresponded to subsets that were noticeable on the field. For spiders, we applied the method of functional entities since all traits were categorical, and each unique combination of traits resulted in a distinct group (Mouillot et al., 2014). Thus, we identified 35 functional entities (Table S4). We run the further analyses with these groups for plants and spiders, but note that we also run the analyses with groups defined *a priori*, to ensure that our results were not trivially the reflection of group selection. For plants, we adapted the "biological types" of species recorded in the French flora database (Baseflor; Julve, 1998), which are derived from the classification of Raunkier, and we partitioned the species into 12 groups. For spiders, we used the guilds' typology developed by Cardoso et al. (2011), and we partitioned the species into 7 groups. With this alternative group selection, we obtained the same results hereafter for both plants and spiders (Figure S4).

Sampling effort

Before calculating species co-occurrence probabilities to estimate dark diversity, we tested the sampling effort of our datasets, to validate the fact that the data satisfactorily mirrors the structure and composition of sampled communities. This is particularly advised when sampled units are limited (Lewis et al., 2016; Pärtel, 2014) because in such cases assessment of co-occurrence probabilities may provide spurious results (De Cáceres & Legendre 2008). Sampling effort estimation is assessed as the average ratio between observed and estimated richness with several richness estimators (Soberón et al., 2007), namely Abundance Coverage-based Estimator (ACE), Bootstrap, Chao, Incidence Coverage-based Estimator (ICE)

and Jackknife 1. Our datasets being rather well sampled, with average coverage degrees greater than 80% (see Figure S5), we considered possible to assess dark diversity using all species.

Measuring dark diversity and completeness

First of all, we measured the taxonomic and functional, observed diversity of communities, that is, species and functional group richness.

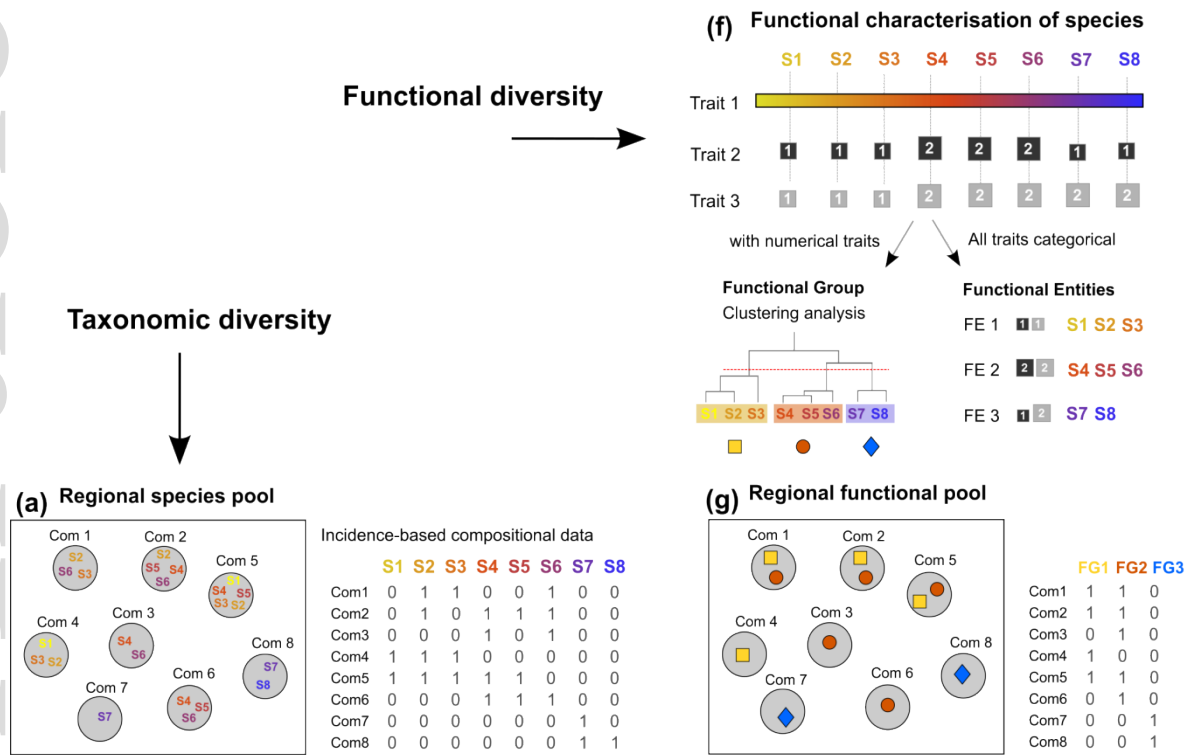
Then, we calculated dark diversity using the Beals co-occurrence index (Beals, 1984), which is the most widely used method (Belinchón et al., 2020; Lewis et al., 2016). This method estimates dark diversity by calculating the probability that a species occurs in a plot based on its co-occurrence with the observed species in the rest of the dataset. A species is thus considered to be part of the dark diversity of a plot if it is absent in the plot but regularly co-occurs with species which are present in the plot. Beals' probabilities increase with species frequency: the more a species occurs in the dataset, the higher the probability of identifying associations with others (De Cáceres & Legendre 2008; Münzbergová & Herben 2004). Therefore, to ensure that dark diversity is not simply the reverse of species rarity, the definition of a probability species-specific threshold is needed to determine whether the species must be included into the dark diversity (=1) or not (=0), resulting in a binary classification (Münzbergová & Herben 2004). This threshold is determined by analysing, for each species, the distribution of Beals' probabilities in the occupied plots, thus allowing these values to be matched with the actual distribution of species. When a species absent in a plot had a probability of occurring in the plot greater or equal to the minimum probability of the other species which are present in the plot, this is interpreted as the fact that the recruitment of this species is possible, and it is hence integrated into dark diversity (Figure 2). We selected the threshold as the 5% quantile of the probabilities (0.05) which is intermediate between broad (0%) and narrow (10%) thresholds, enabling detection of the majority of species while keeping a sufficiently small margin of error (see Lewis et al., 2016). Note that this method can include undesirable species into dark diversity, but given we excluded degraded sites of our design (e.g. marked by biological invasion), we kept all the species to run the analyses.

We adapted this method to calculate functional dark diversity: instead of using taxonomic co-occurrence, we used functional co-occurrence, that is, the probability of functional groups or functional entities to co-occur (Figure 2). The rest of the procedure was identical: we identified in each community the functional groups that were absent while they have an important probability to coexist with the functional groups present in the community. We also calculated, in recent and ancient forests, the occurrence frequency in the dark diversity of each species and each functional group, to analyse how the composition of pools

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differ among both forest types. We also assessed functional dark diversity as it can be basically assessed, that is, from taxonomic dark diversity. Therefore, the analyses of functional dark diversity were proceeded twice: *a priori* (directly) from co-occurrence of functional groups, and *a posteriori* (indirectly) from raw taxonomic dark diversity. Finally, to avoid biased interpretations of the differences in dark diversity due to variations in species richness, we calculated the completeness of communities (Pärtel et al., 2013), that is, their observed diversity relative to their dark diversity. Completeness can be interpreted as a proxy of ecological integrity, and hence can also be used to guide management actions (it is also particularly useful when observed diversity varies importantly among sites). We used the formula: $\ln \left(\frac{\text{observed diversity} + 1}{\text{dark diversity} + 1} \right)$. The numerator and denominator were increased by 1 to avoid the limits of division by zero (Helm et al., 2015).

Step 1: Characterisation of site-by-species and traits datasets



Step 2: Estimation of dark diversity

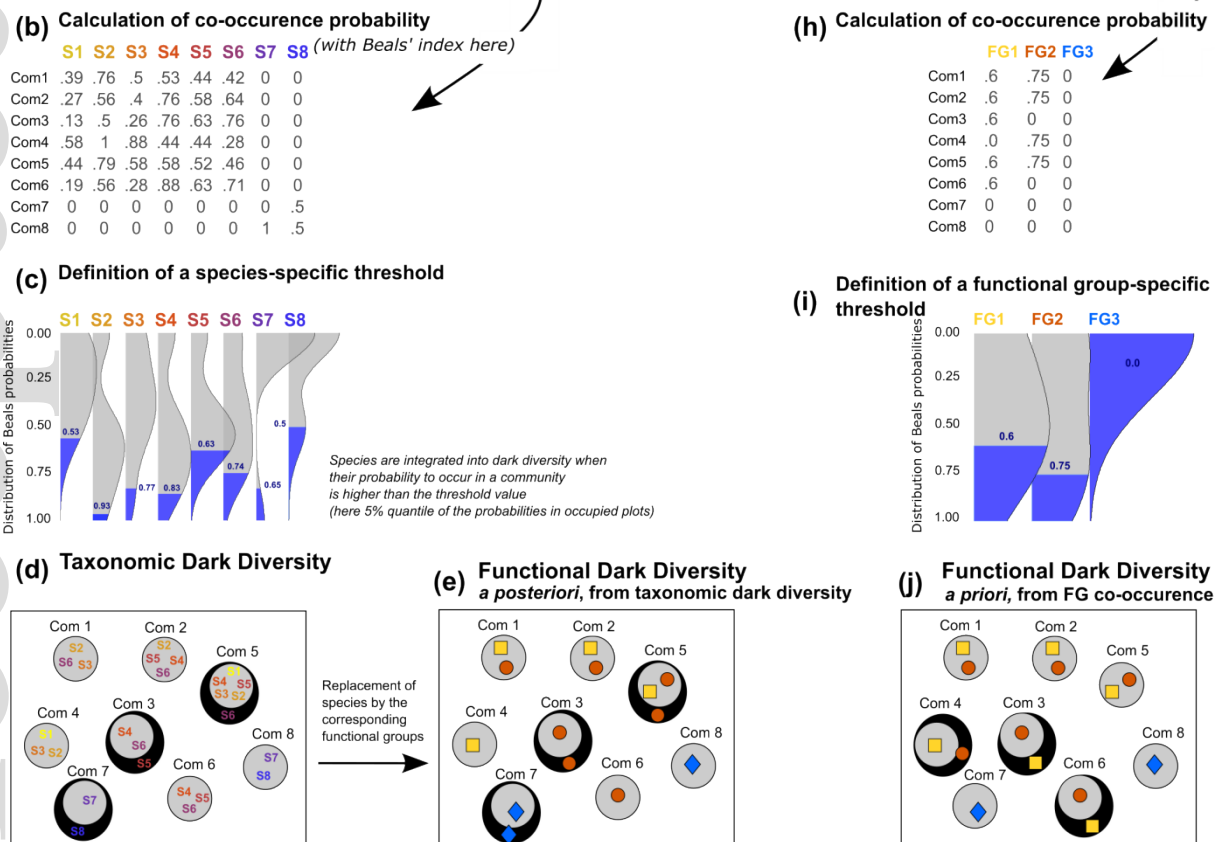


Figure 2. Analysis approach for measuring taxonomic and functional dark diversity with co-occurrence probabilities. “Com1” means community 1 and “S1” means species 1. The dark diversity of each community is represented by a circle with a black background surrounding the observed diversity of communities (a,b,c,d,e) From the presence/absence matrix of species, the Beals index estimates the co-occurrence probability of each species in each community. A species-specific threshold is determined by analysing, for each species, the distribution of Beals probabilities in the occupied plots, and then taxonomic dark diversity is assessed. Taxonomic dark diversity integrates a species when it lacks from the plot but its co-occurrence probability is higher than the threshold value (5% here). Based on this assessment, an indirect estimation of functional dark diversity can be made, by replacing species with the corresponding functional group. (f,g,h,i,j). By using a matrix of functional group co-occurrence (or functional entities), preliminary obtained from functional characterization of species, we can directly estimate functional dark diversity. The methodological principle is identical to that of taxonomic dark diversity, but relies on other data. Note that functional dark diversity assessed indirectly (*a posteriori*) and directly (*a priori*) provide different results.

Data analysis

We had a dataset with a nested structure: replicate plots nested into forest sites, nested into forest types. Therefore, we used generalised linear mixed models (GLMMs with Poisson distribution family) for discrete variables (observed and dark diversity) and linear mixed models (LMMs) for continuous variables (completeness) to test differences among forest types (i.e. ancient versus recent). We used the forest type as a fixed factor and the hierarchical structure (plots nested within sites) as a random effect, to remove any potential effect of autocorrelation. All analyses were performed using R software (R Core Team, 2020). The handling of trait matrices and identification of functional groups were done using the package “cluster” (Maechler et al., 2019) and the “species_to_FE” and “FE_metrics” functions (Mouillot et al., 2014). Richness estimators were computed with the “fossil” package (Vavrek, 2011). The measures of dark diversity were made with the “DarkDiv” package (Carmona & Pärtel, 2020). Statistical tests were performed thanks to the package “lme4” (Bates et al., 2015).

Results

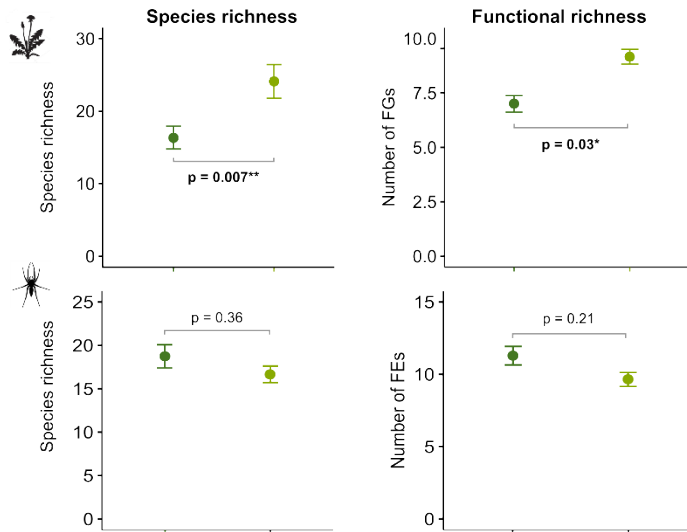
Observed diversity

First, the observed species richness varied importantly among plots, in particular for plants: we recorded from 7 to 41 plant species in the plots studied, and from 10 to 33 spider species. The observed functional richness also varied importantly: from 5 to 10 functional groups of plants, and from 6 to 17 functional entities of spiders (Table S5). The average observed alpha-diversity differed partly between forest types: species richness was significantly higher in recent forests for plants, but not for spiders (Figure 3a). The functional richness showed the same patterns than species richness.

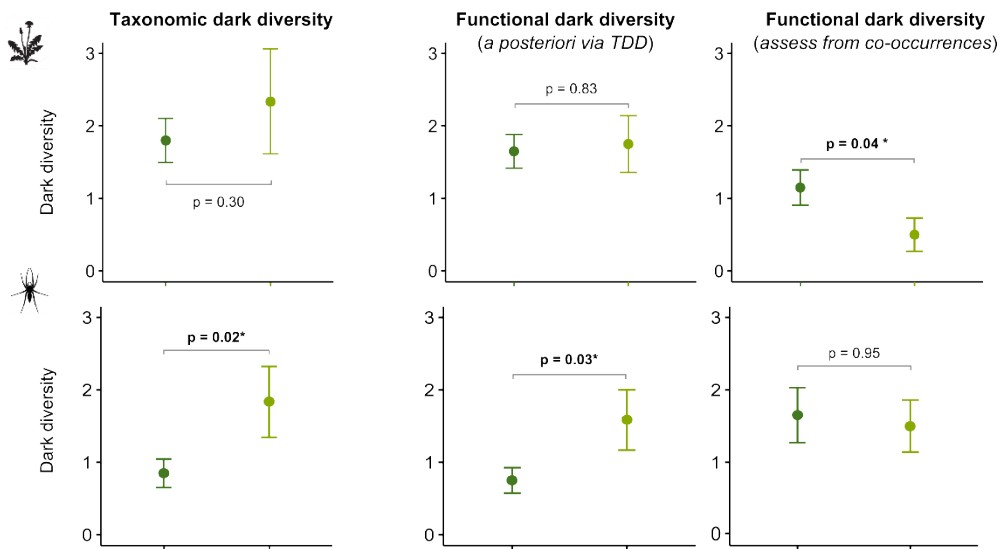
Taxonomic and functional dark diversity

Overall, we found contrasting patterns between ancient and recent forests, and between taxonomic and functional dark diversity (Figure 3b). There were no significant differences of taxonomic dark diversity between recent and ancient forests for plants (2.3 ± 2.5 vs. 1.8 ± 1.4 , $p > 0.05$, Wald's test), but more taxonomic dark diversity in recent forests for spiders (1.8 ± 1.7 vs. 0.9 ± 0.9 , $p < 0.05$, Wald's test). Functional dark diversity calculated *a posteriori* from raw species co-occurrences showed exactly the same patterns than taxonomic dark diversity. However, the direct assessment of functional dark diversity from the co-occurrences of functional groups showed original patterns that systematically differed from taxonomic dark diversity. In particular, the differences between ancient and recent forests in terms of taxonomic and functional dark diversity were opposite, both in sign and magnitude. For plants, we found no differences in taxonomic dark diversity between ancient and recent forests, but we found more functional dark diversity in ancient forests (1.2 ± 1.1 vs. 0.5 ± 0.8 , $p < 0.05$, Wald's test). For spiders, there were more taxonomic dark diversity in recent forests than in ancient ones, but no differences for functional dark diversity (1.5 ± 1.2 vs. 1.7 ± 1.7 , $p > 0.05$, Wald's test). Results of completeness showed entirely similar patterns compared to patterns of dark diversity, except for spiders at the taxonomic level (Figure 3c). In this precise case, the completeness pattern was however partly consistent with those of dark diversity since the difference between ancient and recent forests was slightly non-significant (see Figure 3c).

(a) Observed diversity



(b) Dark diversity



(c) Completeness

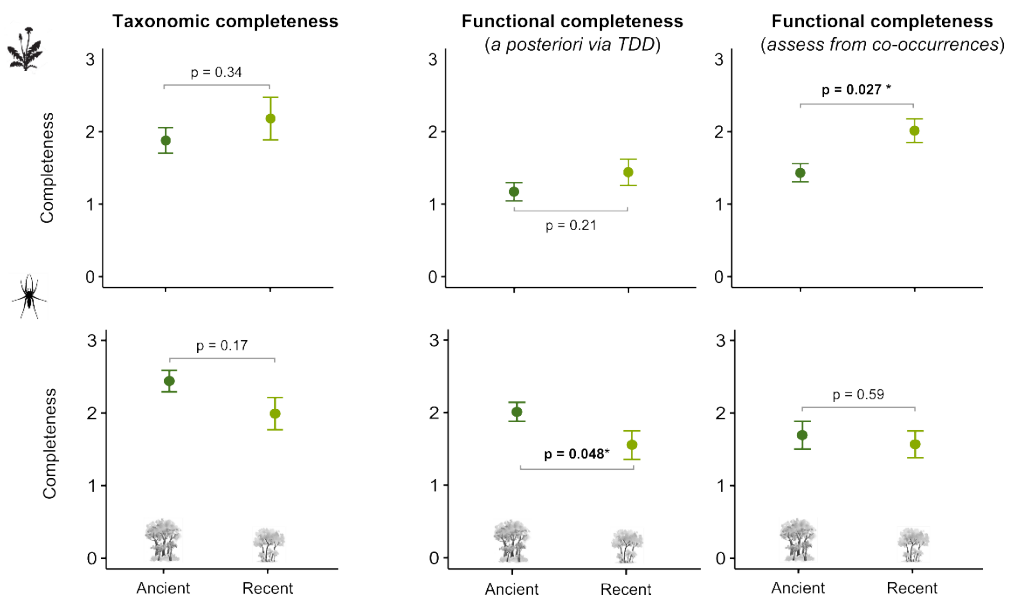
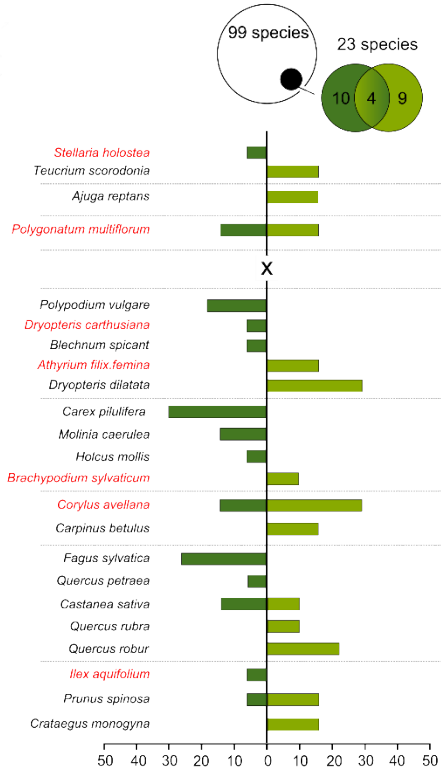


Figure 3. Comparisons of observed diversity (a), dark diversity (b) and completeness (c) between ancient and recent forests, for plant and spider communities, and for the taxonomic and the functional facets. Functional dark diversity and completeness are calculated *a posteriori* (indirectly) from raw taxonomic dark diversity, and *a priori* (directly) from co-occurrence of functional groups. Note that dark diversity is basically not the converse of observed diversity.

Composition of dark diversity

In total, 23 plant species (23% of the species pool) and 23 spider species (26% of the species pool) were recorded at least once in the taxonomic dark diversity (Figure 4). Also, 6 functional groups of plants (60% of the pool of functional groups) and 16 functional entities of spiders (46% of the pool of functional entities) were recorded at least once in the functional dark diversity (Figure 4). Overall, the composition of taxonomic and functional dark diversity strongly differed between forest types (Figure 4): only 4 plant species, 4 spider species, 3 plant functional groups and 9 spider functional entities were observed in the dark diversity of both forest types. 10 plant species and 2 plant functional groups (mesophanerophytes and vernal geophytes) were specific to the dark diversity of ancient forests, whereas 9 plant species and one plant functional group (megaphanerophytes) were specific to the dark diversity of recent forests. Furthermore, 11 spider species and 6 spider functional entities were specific to the dark diversity of ancient forests, and 8 spider species and one spider functional entity were specific to the dark diversity of recent forests. In particular, we observed that some groups were present in the functional dark diversity while their species, which were infrequent, were absent in the taxonomic dark diversity (Figure 4). We also observed the opposite result: some species were present in the dark diversity while their functional groups were not.

(a) Taxonomic dark diversity



(b) Functional dark diversity

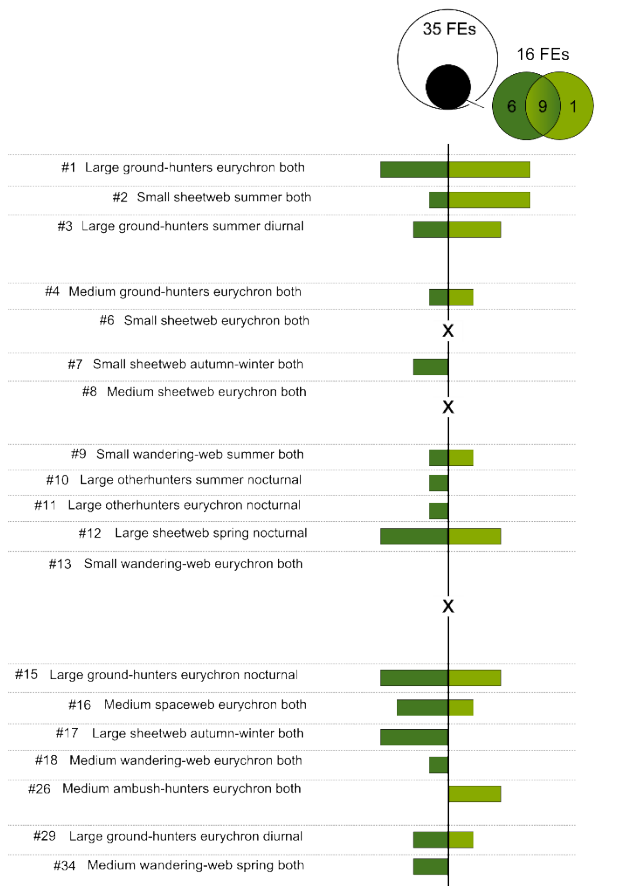
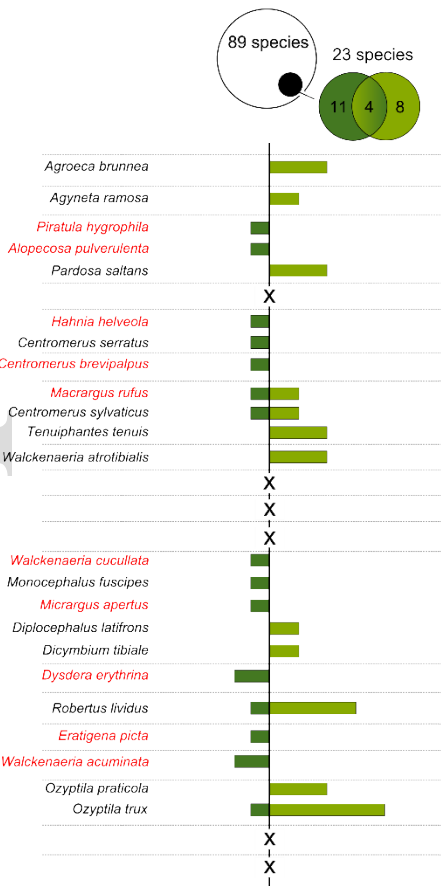
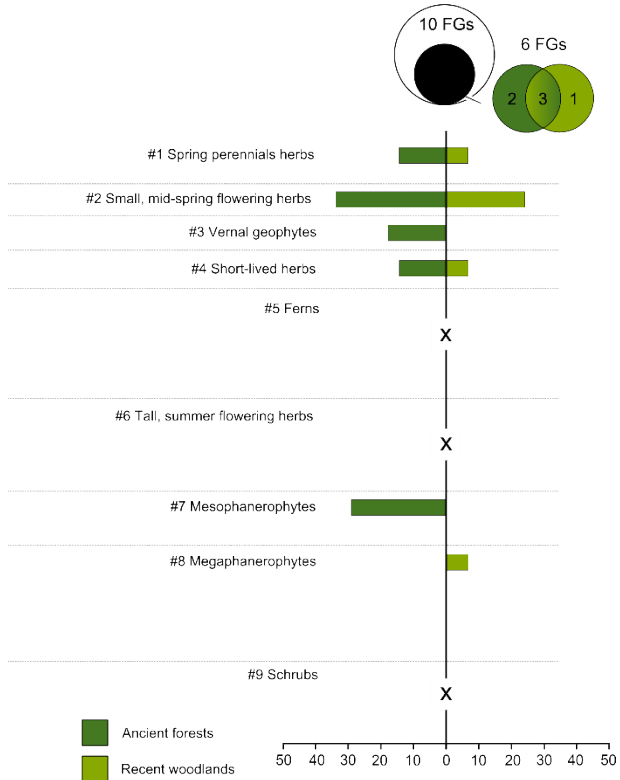


Figure 4. Occurrence frequency in the dark diversity of ancient and recent forests of (a) species of plants and spiders and (b) functional groups (FGs) of plants and functional entities (FEs) of spiders. Occurrence frequency is calculated, for each forest type, as the percentage of plots where a species/FG/FE is recorded in the dark diversity. Functional dark diversity is estimated *a priori*, using co-occurrence of functional groups (see Figure 1 & 2). Only groups, entities and species observed at least once in the dark diversity are presented. Species usually more frequent in ancient forests are in red (from Hermy et al., 1999 and Morel et al., 2019a for plants and spiders, respectively). Black crosses indicate absence in the dark diversity. See Figure S1 and Table S4 for more details on functional groups and entities. See also Table S5 for comparison of species and FG/FE occurrence frequency in observed diversity.

Discussion

Our application of the dark diversity framework into a case study of passive rewilding revealed several novel ecological insights, and suggested the mechanisms involved in the re-assembly of natural communities after land-use changes. The combined use of taxonomic and functional approaches enabled a more complete ecological diagnostic, informing both the past and the potential future of natural communities. In particular, the direct quantification of functional dark diversity brought new light on the potential abilities of recent woodlands to spontaneously recover native forest biodiversity: we demonstrated that, surprisingly, recent forests were in fact quite complete from an overall, ecological perspective. Despite lacking specialist, plant and spider species, recent woodlands already harboured functionally rich communities.

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

Our results obtained from functional dark diversity that was directly assessed from functional group co-occurrence clearly differed from those obtained from taxonomic dark diversity. For plants and spiders, the taxonomic approach integrated only one quarter of all species into dark diversity, whereas about half of all functional groups were integrated at least once into functional dark diversity (Figure 3). Thus, our results suggest that an exclusively taxonomic approach (or a functional approach derived from taxonomic dark diversity) tends in fact to overestimate the ecological integrity of communities, by missing out the fact that some niches are actually vacant in several communities. For example, no species of short-lived herbs (FG #4) or medium-size generalist hunting spiders (FE #4) was ever integrated into taxonomic dark diversity, while these groups were often integrated into functional dark diversity (Figure

3). Overall, all these results showed that our approach increased the probability of detecting the absence of functional features hosted by rare species, whereas neither taxonomic dark diversity nor a functional interpretation of it could detect them (as we supposed, see Figure 1d). This is particularly well illustrated in the case of plants: when we re-run the analyses without rare species (i.e. whose occurrence is less than the first quartile of the species distribution), there were no longer any differences of functional dark diversity between ancient and recent forests, whether calculated a priori or directly (2 ± 0.9 vs 2.6 ± 1.3 for FDD a posteriori, and 0.9 ± 0.6 vs 0.7 ± 1.2 for FDD directly assessed, $p > 0.05$, Wald's test). Our approach appears hence particularly useful in habitats where many infrequent species provide similar functions.

On the other hand, functional dark diversity as we calculated it might, also, overestimate the ecological integrity of natural communities, because it considers communities represented by a single species per group as complete (see Figure 1b). Thus, species may be lacking but their respective groups may not: for example, shrubs and ferns were never included into dark diversity, whereas some of their species were (Figure 4). In our study, this consideration of the functional redundancy also clearly influenced the patterns of functional dark diversity of spiders (Figure S6). We could hence summarise our approach in simple words: functional dark diversity is not interested in species. This can be a major advantage: for habitat conservation and restoration, it is often crucial to investigate ecosystem functioning and related services before assessing their richness or originality in species (Cadotte et al., 2011). However, this could be a drawback in other cases: conservation and restoration policies can also target species for their intrinsic patrimonial value (existence values), hence requiring consideration of species identities. Rare species may also play a key role in ecosystem functioning by ensuring singular functions or enhancing functional redundancy (Chapman et al., 2018; Leitão et al., 2016). We hence suggest that further methods need to be developed to measure the potential regeneration of natural habitats considering rare species with rare functional features. Overall, we think that taxonomic dark diversity and functional dark diversity illustrate different facets of communities, and that they can be very complementary metrics which, taken together, provide reliable information for ecological diagnostic and for conservation and restoration policies.

Functional dark diversity reveals a greater importance of dispersal limitation than taxonomic dark diversity suggests

The combined use of taxonomic and functional dark diversity enabled to explore the assembly processes that shaped our communities of recent and ancient forests. First, our results confirmed that recent woodlands, even after decades of forest re-establishing, do not fully recover communities like those of

ancient forests in terms of species identity, whether for plants (Bergès & Dupouey, 2020; Hermy & Verheyen, 2007) or spiders (Morel et al., 2019a). Dark diversity showed that recent forests mainly lacked some generalist species they could recruit (e.g. phanerophytes or ruderal-nitrophilous plants such as *Crataegus monogyna* and *Ajuga reptans*, and several ubiquitous hunter spiders such as *Agroeca brunnea* and *Pardosa saltans*). Moreover, we observed that recent forests also lacked specialist forest species, but they might not be able to be recruited, since they were not identified in their dark diversity. These specialists, which are mainly slow-colonisers associated with unique, restricted ecological conditions (e.g. oligotrophic and acidophil soils for plants, Hermy & Verheyen, 2007, and complex litters associated to dead-wood materials for spiders, Morel et al., 2019a) were almost exclusively associated, when they were absent, to ancient forests. Consequently, we observed compositional differences between the dark diversity of recent and ancient forests, regardless of their observed richness, indicating that recruitment conditions changed, probably due to past land uses. This put recent woodlands on a different ecological trajectory, that still impeaches a substantial recruitment of specialist species. Moreover, we also observed that dispersal limitation affected some generalist species of recent woodlands and some specialist species of ancient forests (i.e. the species which were detected in the dark diversity). We note, as has been observed in other contexts (Moeslund et al., 2017, Belinchón et al., 2020), that these species generally have lower dispersal capacities, such as barochory or myrmechocory species (e.g. *Teucrium scorodonia*, *Carex pilulifera*) or, in the case of spiders, large-size species less suitable for dispersal by ballooning (e.g. *Agroeca brunnea*).

On the other hand, the fact that, in proportion, much more functional groups were included into dark diversities than species (Figure 4), suggests that the compositional differences between both forests are not as important as the taxonomic approach suggests. Yet, contrary to taxonomic dark diversity, functional dark diversity focuses on deterministic processes and is mainly insensitive to ecological drift, so the presence of several functional groups in the dark diversity of both forest types definitely showed that dispersal limitation was a strong driver of the assembly of their communities (dispersal limitation can be confounded with ecological drift with an only taxonomic approach). This result highlights the existence of a significant “functional colonisation credit”: to some extent at least, some spider guilds (e.g. litter ambush hunters) and functional plant types (e.g. small mid-spring herbs) typical of ancient forests can be actually recruited within these recent forests.

Beyond these compositional changes, functional dark diversity showed that recent woodlands harboured diverse communities which were quite complete from a functional perspective, especially regarding plants. Recent woodlands thus mainly lacked small springs herbs whereas ancient forests also lacked

shrubs, vernal geophytes and various herbs. Since ancient forests are generally less constrained by dispersal limitations (because there has not experimented a rupture of the temporal continuity), it is more likely that these differences are attributable to variations in the intensity of niche selection between the two types of forests. In this sense, three additional hypotheses could explain why the selection would be lower in recent forests and thus lead to increase the number of groups that can be recruited. First, recent woodlands might temporary harbour "relictual species" (and their functional features) inherited from preceding successional stages (shrubs species typically), which might be in extinction debt and could disappear with time (Bagaria et al., 2015). Second, past land uses may have reduced nutrient limitation through soil fertilisation, particularly on the acid soils of our study region (Graae, 2000; Koerner et al., 1997), leading to recruitment of more diverse functional features in recent woodlands (Morel et al., 2019b). Last, past management of forests might play a great role: since several centuries, the management of ancient forests has shifted from coppicing to high-forest system, which has tended to disadvantage shade-loving, understorey woody and herb species (Kirby & Watkins, 2015). On the contrary, recent woodlands conserve a denser coppice, thus leading to a lower amount of light reaching their understorey (illustrated by the Ellenberg values, Table S1), which could enrich the herbaceous cover in terms of both species and functional plant features. According to these last two hypotheses related to a modification of the niche selection, compositional and structural differences between both forest types should be maintained with time.

Overall, our results reveal the extent to which dispersal limitations, in addition to recruitment limitations, drive the compositional differences observed between two sets of ancient and recent forests. From a conservation perspective, the potential diversity of the recent woodlands revealed here, suggested that they were already in quite good ecological conditions. Thus, these results may challenge and improve our perception of the conservation value of both recent and ancient forests: recent woodlands do lack typical ancient forest species, but they can also recover functionally rich and ecologically complete communities. Even if forestry is not incompatible with biodiversity, we think that an increase in wildwood areas could benefit to conservation of forest ecosystems.

Perspectives and limitations

We argue for the development of the framework of functional dark diversity for both researchers and practitioners, notably in the study of biodiversity responses to land-use changes. We acknowledge some limitations of our results: our recent study forests might be in somewhat good conditions compared to other ones elsewhere in the study region, because they have not undergone a particularly excessive anthropogenic pressure during their regeneration. We also note that we studied dark diversity on a

relatively small dataset (i.e. eight forests of Brittany), but we think it was sufficiently robust to analyse the different facets of dark diversity and test their dissemblances. Overall, we think that our method assessing directly functional dark diversity, with its simplicity, can easily be applied to many other issues of conservation and restoration. The combined use of functional and taxonomic dark diversity can deal with the assessment of the ecological integrity of natural communities, both from a functional perspective (including resistance and resilience capacities of ecosystems) and from a taxonomic one (e.g. recruitment of species with particular interest). The results given by both approaches may hence help to define the most interesting sites to acquire for conservation and restoration plans, and also prioritise management efforts among sites that are already managed. Our functional approach may be particularly useful for habitats that are very degraded and lack a lot of functional features: in this case, the restoration of ecological functions, for example through the restoration of the optimal niche conditions for species providing these functions, is the priority objective of restoration plans. Our approach enables to accurately diagnose the potential ecological functions of degraded communities and hence identify the management actions that will be the most efficient in (re-)establishing these functions. Since the method is entirely based on the co-occurrence of functional groups, the choice of these functional groups is a central concern. We ensured that functional groups satisfied two conditions: functional variation must be minimised within groups and maximised between groups, and co-occurrences within groups had to be less deterministic than between groups. We also ensured that the selected functional groups corresponded to a precise ecological compartment, that is, a subset of species that was noticeable in the field. In this way, we think that the functional group approach for dark diversity may be used, and does have a biological sense. The use of our functional approach greatly reduced the risk of not detecting functional features hosted by rare species, but note that our approach does not completely solve the problem if the functional features are themselves rare. Further methods could be developed in the future, using a continuous approach for traits along the whole calculation process, or focusing on the specialisation degree, the evolutionary distinctiveness or the functional originality of species present in the dark diversity.

Authors' contributions

LM conceived the ideas. LM initiated and framed methodology, with inputs from LB, VJ and SC. LM and FY collected the data. LM conceived and performed the analyses. LM and LB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of interest

The authors have declared no conflict of interest.

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Data availability statement

Data available via the Figshare public repository <https://doi.org/10.6084/m9.figshare.16611526.v1> (Morel L., 2021).

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