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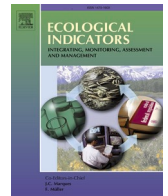
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Dark diversity and habitat conservation status: Two sides of the same coin for conservation and restoration?

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ABSTRACT

The current biodiversity crisis calls for an acceleration in the implementation of measures to conserve and restore ecosystems around the world. To achieve these objectives, it is imperative to provide scientifically robust tools that practitioners can easily apply. In recent years, two theoretical frameworks have been proposed, habitat-specific species pools and dark diversity. The aim of our study is to assess the value of combining these two concepts in order to improve predictions of dark diversity by restricting estimates to the pool of species typical of the habitat. Our study focuses on two habitats, heathlands and grasslands, both of which present major conservation and restoration challenges. We carried out vegetation surveys in 290 heathlands and 425 grasslands spread throughout the region. Our results indicate that restricting dark diversity estimates to the habitat-specific species pool significantly reduces the number of species estimated in dark diversity. Furthermore, we show that a large proportion of the species predicted in the dark diversity are species nontypical of the studied habitats. Our results also demonstrate that there is no redundancy between approaches based on the assessment of observed conservation status and those based on dark diversity. The use of the dark diversity is complementary to approach based on the assessment of observed conservation status for the diagnosis, prioritisation and monitoring of conservation or restoration measures. Nevertheless, our results indicate that in the context of conservation and restoration, estimates of dark diversity must be restricted to the habitat-specific species pool.

1. Introduction

The current biodiversity crisis we are facing implies huge habitat conservation and restoration efforts in order to bend the curve of biodiversity loss (Aronson et al. 2020; Leclère et al. 2020; Cowie et al. 2022; Finn et al. 2023). Traditionally, observed species diversity is used to assess both the need and success of habitat conservation and restoration (Beechie et al. 2008; Shackelford et al. 2013; Helm et al. 2015). The underlying idea is that habitats with the higher diversity are the priority to conserve, and conversely, habitats with the lower level of diversity are the more in need for restoration. So, for example, if we have to choose between two patches of grassland to conserve, choosing the one with the highest diversity seems the best option. However, this is only true if the species responsible for the higher diversity in the first site are species typical from grassland, and not, for example, successional species such as pioneer trees and bushes, or exotic species. Indeed, such species, although reflecting habitat degradation, can nevertheless lead

to an inflation of species richness. On the other hand, we could also argue that choosing the site to conserve or restore based on observed diversity or the presence of rare species is maybe not the best option because some sites may have low expressed diversity but strong potential for improvement. Indeed, current management measures (e.g. excessive mowing frequency) may prevent the expression of species despite the site's high potential, leading to a biased diagnosis of conservation and restoration priorities if we base our decisions solely on the expressed diversity. One of the major challenges for scientists is therefore to propose metrics to improve the planning, diagnosis, and success of management and restoration operations (Lamb et al. 2009; de Bello et al. 2010; Török and Helm 2017; Evju et al. 2020).

Two relatively recent concept, habitat-specific species pool (Zobel 2016) and dark diversity (Pärtel et al. 2011) could help us to deal with the previously mentioned issues and improve our conservation and restoration practices. The former defines a set of species that occur naturally in a region, are theoretically able to disperse to the studied site

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and have functional traits that enable them to survive and reproduce in the particular habitat (Eriksson 1993; Pärtel et al. 1996). Recent studies have emphasized the importance of including the habitat-specific species pool for conservation (e.g. Bonari et al. 2021; Dalle Fratte and Cerabolini 2023; Bricca et al. 2024), and more specifically to distinguish between observed species that belong to the habitat-specific species pool (or 'typical species') and those that do not (or 'nontypical species', Jung et al. 2021). These studies have proposed new metrics based on species presence/absence (Helm et al. 2015) or abundance (Jung et al. 2021) for assessing the conservation status of habitats, which have proven highly effective for evaluating management or restoration (Napoleone et al. 2021; Chollet et al. 2023). Dark diversity is defined as the part of the diversity of a site that is currently absent, although the species could become established there (Pärtel et al. 2011). Numerous reasons could explain why some species presenting relevant suits of traits are absent from a site. Species could be absent because they were unable to reach the site (dispersion limitation), due to ecological drift (demographic stochasticity), or priority effect at arrival to the site (competitive exclusion due to historical stochasticity). In addition to these natural causes, human activities could strongly increase the dark diversity of a site by increasing fragmentation of habitats, by inadequate management (e.g., fertilization, mowing, etc.), or by introducing exotic species (Trindade et al. 2020). Dark diversity can be particularly useful for conservation and restoration because it can highlight locally absent species. Although usually neglected, these absences are in fact informative, as they tell us both about the potential of a site (Pärtel et al. 2011) and about the species themselves, by studying the characteristics of those included in the dark diversity (Moeslund et al. 2017). In practice, the concept can therefore be used to determine: sites with the highest conservation values due to their completeness with regard to the habitat species pool (i.e. reflected by species poor dark diversity, Lewis et al. 2017); sites with the greatest potential for restoration (Gijbels et al. 2012) or the greatest risk of invasion (Bennett et al. 2016; Ronk et al. 2017). Furthermore, dark diversity can also be an interesting metric for monitoring management or restoration operations (Noreika et al. 2020; Morel et al. 2022) or assessing colonisation credit (Gijbels et al. 2012). However, to date, dark diversity has been underused in conservation and restoration, which may be due to certain estimation pitfalls that make the concept difficult to implement and not fully operational for practitioners.

Several methods have been proposed to estimate dark diversity of a site, based on species ecological affinities (e.g., using Ellenberg indicator values) or species co-occurrence patterns, with the latter shown to be more accurate (Lewis et al. 2016). The idea behind the co-occurrence method is that species which usually co-occur have similar ecological requirements (Pärtel et al. 2011; Riibak et al. 2015). If, at a particular site, one of the species frequently present with the other species observed is absent, it will be considered to be part of the dark diversity of the focal community (Ronk et al. 2015). Among the proposed method, the use of pairwise co-occurrence data with a hypergeometric distribution offer a flexible and robust estimates of probabilistic dark diversity (Carmona and Pärtel 2021; Paganeli et al. 2024). However, in the case of habitat conservation and/or restoration, the methods based on species co-occurrence patterns (hereafter referred to as "co-occurrence methods") could induce pitfall when they are used without explicitly taking account of habitat-specific species pools. In general, conservation/restoration actions are targeted on a particular type of habitat, with the aim of seeing the reestablishment of species typical of that habitat. However, co-occurrence methods (as they are usually used) can include in the dark diversity species that do not belong to the habitat species pool, and which are therefore not really relevant in a conservation/restoration context. The first reason is that habitats of conservation and/or restoration interest host numerous nontypical species (Fig. 1A). In fact, in sites of conservation interest and even more so in sites with a need for restoration, habitat degradation is reflected by the presence of species that are not typical of the habitat. Therefore, if we estimate dark

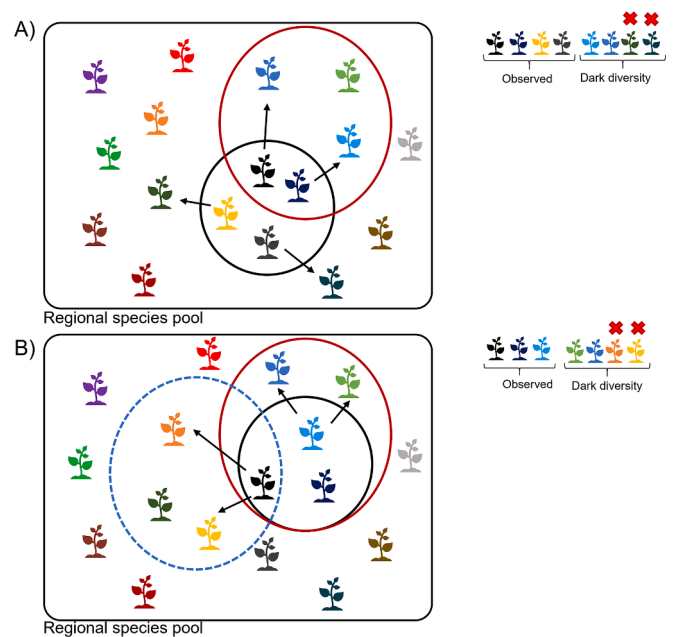


Fig. 1. Two theoretical situations in which estimating dark diversity using co-occurrence methods can pose problems in the context of conservation or restoration. The black rectangle represents the regional species pool, with each species represented by a different colour. The habitat specific species pools are represented by the red and blue circles. The observed community is represented by the black circle. In case (A), only two of the four observed species belong to the habitat-specific species pool (red circle), leading to an overestimate of dark diversity by including species co-occurring often with nontypical species (species with red crosses). In case (B), all the species observed belong to the habitat-specific species pool, but one of the species also belongs to another habitat-specific species pool (blue circle), leading to the inclusion of species typical of this second pool (species with red crosses). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

diversity in these sites, co-occurrence methods will predict a high dark diversity, with an important proportion of nontypical species. Moreover, even in the case of a well-preserved site hosting only typical species, co-occurrence methods can still include nontypical species in the dark diversity, due to the potential overlap between different habitat-specific species pools (Fig. 1B). Indeed, some species may belong to several habitat specific species pools (Nicod et al. 2019; Rodríguez-Rojo et al. 2020) and consequently co-occur with a different set of species in each. In both cases the result will be the same, an overestimation of dark diversity richness due to the prediction of nontypical species, reducing the interest of using this approach for conservation and restoration practitioners.

Finally, as conservation and restoration are implicitly based on a dichotomy between typical and nontypical species, we argue that this dichotomy should be explicitly implemented in dark diversity in order to make this concept applicable in these fields. We therefore propose that dark diversity estimation should be made restricting the co-occurrence pattern analysis to the habitat-specific species pool. Theoretically, this method will reduce the amount of predicted dark diversity richness by predicting only typical species, consequently increasing the interest for conservation and restoration. In addition, in order to promote the use of dark diversity in applied ecology, it is necessary to demonstrate that metrics evaluating conservation status of habitats from observed species are not fully redundant – and are even complementary – with dark diversity information. It may seem obvious that sites in favourable conservation status (i.e., where typical species dominate over nontypical species) tend to have fewer typical species in the dark diversity (i.e. a high completeness, Pärtel et al. 2013) than sites with low conservation

status (Fig. 2A). However, we can hypothesize that any combinations of habitat conservation status and dark diversity (or completeness) are possible, which has important implications for conservation planning. Indeed, a degraded site with a low dark diversity (Fig. 2B) may not represent a restoration priority compared to a degraded site with a high dark diversity. However, if a well-preserved site can have a high dark diversity (Fig. 2C), this may indicate that it still has potential for improvement through the application of appropriate management.

We tested the relevance of reducing estimates of dark diversity to the habitat's specific pool and the complementarity of these metrics with those of habitat conservation status in two habitats in Brittany: heathlands and grasslands. Both are seminatural habitats of high conservation values that host rare and typical species (Fagúndez 2013; Habel et al. 2013). However, since the Second World War, both habitats have faced similar threats consisting of abandonment or intensification, but in a different proportion. Management in grassland was intensified mainly with increasing mowing or grazing pressures, often accompanied by drainage and inorganic fertilization (Green 1990; Blüthgen et al. 2012). Only less productive or uneasily mechanizable grasslands were abandoned (Habel et al. 2013). On the other hand, heathlands traditionally used as extensive grazing ground were abandoned for most of them, inducing colonization by forest species (Kepfer-Rojas et al. 2017), but a few were converted to meadows (Fagúndez 2013). In all cases, these change in practices induce a colonization by species not typical of the habitats (e.g., species indicating high soil nitrogen content or overgrazing in grassland, species indicating natural succession to forest in heathland). Our main objective was to investigate how dark diversity and habitat conservation status could be used to evaluate conservation efficiency and restoration planification in these habitats. First, we intend to verify that reducing the estimate of dark diversity to the habitat's specific species pool does indeed lead to a significant reduction in the number of estimated species. Second, we assess whether there is any redundancy between the metrics used to assess observed conservation status and those derived from dark diversity. Finally, through specific case studies in protected areas, our aim is to demonstrate the

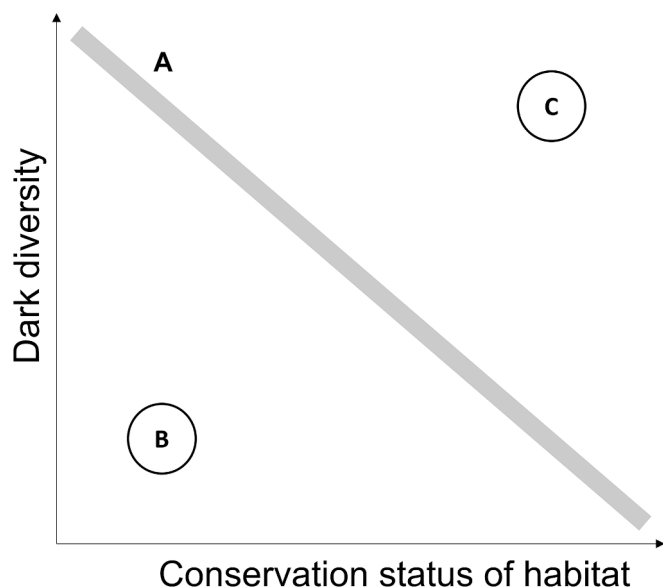


Fig. 2. Relationship between the conservation status assessed from the observed species and typical species richness found in the dark diversity. The bold grey line (A) represents the most obvious situations where well-preserved sites tend to have low dark diversity. The situation (B) a degraded site with a low dark diversity and (C) a well-preserved site with a high dark diversity correspond to the most interesting situations for conservation, i.e. situations where dark diversity information is particularly complementary to the evaluation of habitat conservation status.

complementarity of approaches based on observed conservation status and dark diversity for conservation and restoration.

2. Materials & methods

2.1. Study region and data sets

Brittany is a region located in north western France that presents an oceanic climate, characterized by a low amplitude in temperature between seasons (4° C on average in winter, 22° C on average in summer) and precipitations (1000 mm on average) well distributed year-round (Météo France). The topography is relatively flat due to the old age of the Armorican massif, formed during the Variscan orogeny (Le Corre et al. 1991; Ballèvre et al. 2009). The relief is made up of small hills (culminating at 385 m above sea level) interspersed with wet valleys due to the impermeability of the substrate (Corillion 1971). The dominance of granitic and sandstone bedrocks has led to the development of acid soils. The original typical vegetation was characterized by acidic forests that have been cleared for agriculture since the bronze age (David 2014). This resulted in the development of grasslands and heathlands that dominated the landscape for centuries, before declining dramatically since the Second World War due to a change in traditional farming practices. In this study, we used two large datasets from heathland and grassland communities composed, respectively, of 290 plots (size range 10–50 m², mean = 17.6, sd = 4.3) and 421 plots (size range 10–50 m², mean = 25.3, sd = 6.1), all located in Brittany. Both datasets were composed of two sub-datasets, a first one collected in a large number of sites in order to represent the diversity of the habitats at regional scale (regional dataset hereafter, including 150 heathland plots and 333 grassland plots), and a second one collected as a case study. With the heathland case study, we evaluated the effect of management in one of the largest heathland complexes in Brittany, the protected Vallée du Canut area (500 ha). At this site we surveyed 140 heathland plots, 50 of which were in areas actively managed by conservationists (i.e., bushes and tree removal) and 90 in areas unmanaged for at least 50 years. The grassland case study comprised 92 plots and was carried out to prioritize conservation and restoration needs in six protected areas in eastern Brittany (Boulet [n = 6], Canut [n = 19], Careil [n = 18], Gannedel [n = 35], Gaudriers [n = 6], Jaunouse [n = 7]).

In all heathland and grassland plots, each species of vascular plant was recorded and the abundance was estimated using the Braun-Blanquet cover scale. For quantitative analysis, we used the median % of the Braun-Blanquet scale index.

2.2. Determination of habitat-specific species pool

It is important to note that the species pool of a given habitat includes not only species exclusive to that habitat but also more generalist species, which may belong to the species pool of other habitats. For example, for heathlands, species from the genus *Erica* (exclusive to heathlands) and *Molinia* (which can occupy other habitats) both belong to the habitat-specific species pool. As proposed by Helm et al. (2015) we used a two-step procedure in order to determine the composition of each habitat-specific species pool. First, we used published list of species belonging to heathland or grassland specific species pool (Des Abbayes et al. 1971; Bensettiti et al. 2002, 2005; Diard 2005). In a second time we asked regional flora experts to independently validate our classification. The resulting classification included three categories: species classified as typical species (which are 'normal' to find in the habitat, independently of their rarity or specificity to the habitat) or nontypical species (which are not 'normal' to find in the habitat, reflecting, for example, overexploitation or abandonment). A third category, neutral species, was used for some species of very low frequency and abundance, which were difficult to classify in one or the other of the previous two categories. The classification process resulted, respectively, in 53 and 130 typical species, 63 and 236 nontypical species, 11 and 67 neutral species

in heathland and grassland specific species pool. The detailed list of species in each habitat and their classification is accessible in [Appendix S1](#) in [Supporting Information](#).

2.3. Data analysis

Dark diversity was estimated with the hypergeometric method using the cooccurrence approach (Carmona and Pärtel 2021). The probability of a species being in the dark pool was calculated with the package DarkDiv (Carmona 2020). We chose that all species absent from a site with a probability of being in the dark pool greater than 0.9 would be included in the dark diversity. This high threshold makes it possible to avoid the uncertainties associated with probabilities close to 0.5, which are linked either to a real lack of association or a lack of information (e.g. infrequent species, Carmona and Pärtel 2021). In order to study the potential interest of restricting dark diversity estimation, we first calculated the full dark diversity using all cooccurrence among species. In a second time we estimated dark diversity using only the species belonging to the habitat-specific species pool (excluding nontypical and neutral species from the cooccurrence matrix). Two metrics based on dark diversity were used: richness of the dark diversity and community completeness. The latter is a logarithmic ratio expression of dark diversity calculated as: $\ln(\text{observed richness}/\text{dark diversity})$ (Pärtel et al. 2013).

We used two metrics to assess habitat conservation status based on observed diversity, one using species presence (Helm et al. 2015) and the other including species abundance (Jung et al., 2021). The former, the Favourable Conservation Status index (FCSI, $\log(\text{typical species richness}/\text{nontypical species richness})$), is the log-ratio of the number of species typical from the habitat specific species pool observed on the nontypical number of species observed (Helm et al. 2015). The Vegetation Conservation Status (VCS) is derived from the Simpson index and integrates abundance and richness in typical species and abundance in nontypical species, and calculated as follows:

$$VCS = \left[1 - \sum \left(\frac{n_j}{N_T} \right)^2 * \left(\frac{N_T}{N} \right)^2 \right]$$

where n_j is the abundance of each typical species j , N_T is the sum of the abundance of all typical species and N is the sum of the abundance of all species including both typical and nontypical species. Set between 0 and 1, it is maximized for a habitat that contains many typical species observed in equivalent proportions and low abundance of nontypical species. Neutral species were excluded from the calculation for FCSI and VCS.

The comparison between richness in dark diversity with and without restriction to the habitat-specific species pool was carried out on the regional dataset using a nonparametric Wilcoxon rank test. The correlations between the observed and predicted number of nontypical species in the dark diversity, as well as the link between habitat conservation metrics and dark diversity metrics, were evaluated with a Spearman correlation test. Comparison of conservation status and completeness metrics between managed and unmanaged areas of the heathland case study was carried out using a Wilcoxon median comparison test for two independent sample because of the non-normal distribution of the data. For the grassland case study, because of unbalanced sample size among sites and the non-normal distribution of the residuals of the models, non-parametric Kruskal-Wallis tests for multiple independent samples were used to compare the conservation status and dark diversity metrics between the six protected areas. When significant differences were found we used pairwise Wilcoxon test with Bonferroni correction as post hoc test. To check whether our results could be influenced by the different surface areas of the plots, linear relationship between conservation status, dark diversity metrics and plot surface were tested with linear regression model but any significant relationship were found. All statistical analyzes were performed using R (v4.2.2).

3. Results

We found that when the pool was not previously filtered, the proportion of nontypical species in dark diversity was on average of 39 % (ranging from 0 to 100 %) in heathland and 26 % (ranging from 0 to 86 %) in grassland. In both habitats we found that limiting the dark diversity estimation to the habitat-specific species pool significantly reduce the richness of dark diversity (Fig. 3A-C, Heathland: $W = 56549$, $p\text{-value} < 0.001$; Grassland: $W = 133587$, $p\text{-value} < 0.001$). The number of nontypical species observed in a plot was not or really weakly related to the amount of nontypical species predicted in the dark diversity estimated without restriction to the habitat-specific species pool in heathland (Fig. 3B, $r = -0.03$, $p = 0.54$) and grassland (Fig. 3D, $r = 0.23$, $p = 0.001$). Even in the site where any nontypical species were observed, the predicted amount could reach 11 species in heathlands and 12 in meadows (Fig. 3B-D).

We found no significant correlation between the observed conservation status (VCS index) and the richness of dark diversity in heathlands (Fig. 4A, $r = -0.01$, $p > 0.05$) and in grasslands (Fig. 4C, $r = 0.08$, $p > 0.05$). Similarly, the correlation between the VCS index and the completeness index was low in both habitats (heathlands: Fig. 4B, $r = 0.2$, $p < 0.001$; grasslands: Fig. 4D, $r = 0.32$, $p < 0.001$). This absence of strong correlation between observed conservation status and dark diversity metrics was also found when using the FCSI metric (Appendix S2 in [Supporting Information](#)).

We did not observe any difference in observed habitat conservation status (VCS index) between managed and unmanaged heathland plots (Fig. 5A, $W = 1909$, $p > 0.1$). However, using dark diversity, managed heathlands had greater completeness than unmanaged heathlands (Fig. 5B, $W = 1492$, $p < 0.001$).

We found significant differences in the observed habitat conservation status of grasslands (VCS index) between sites (ANOVA, $F\text{-value} = 9.7$, $p < 0.001$). In particular, the Gannedel protected area hosts grasslands with a significantly lower observed conservation status (Fig. 6 A). We also found significant differences among the completeness of the grasslands in the 6 studied sites (ANOVA, $F\text{-value} = 9.8$, $p < 0.001$). However, the sites with significantly lower completeness were Gaudriers and Jaunouse (Fig. 6 B).

4. Discussion

The use of dark diversity by conservation and restoration practitioners offers additional possibilities compared to the use of information obtained solely on observed diversity. However, our results clearly show that, in order to promote its use in conservation and restoration, estimates of dark diversity must be restricted to species belonging to the pool of species typical of the habitat. Furthermore, our results confirm that dark diversity patterns are complementary to observed diversity patterns, improving our understanding of the effects of different management measures and making the prioritisation of conservation or management measures more effective.

4.1. Necessity to reduce dark diversity estimation to species belonging to the habitat-specific species pool

Our results show that reducing dark diversity estimates to species belonging to the habitat-specific species pool significantly reduces the number of species predicted in dark diversity. Prediction of a high proportion of species that are not typical of the studied habitats (close to 40 % in heathland and 30 % in grassland) is a major concern in the context of conservation and restoration. The risk of overestimating dark diversity due to the presence of non-typical species (Fig. 1A) is particularly high in a restoration context where, by definition, sites are in the process of deterioration. Even in well-preserved sites with no or very few nontypical species the use of cooccurrence methods, the most effective to date (Carmona and Pärtel 2021; Paganelli et al. 2024), necessarily

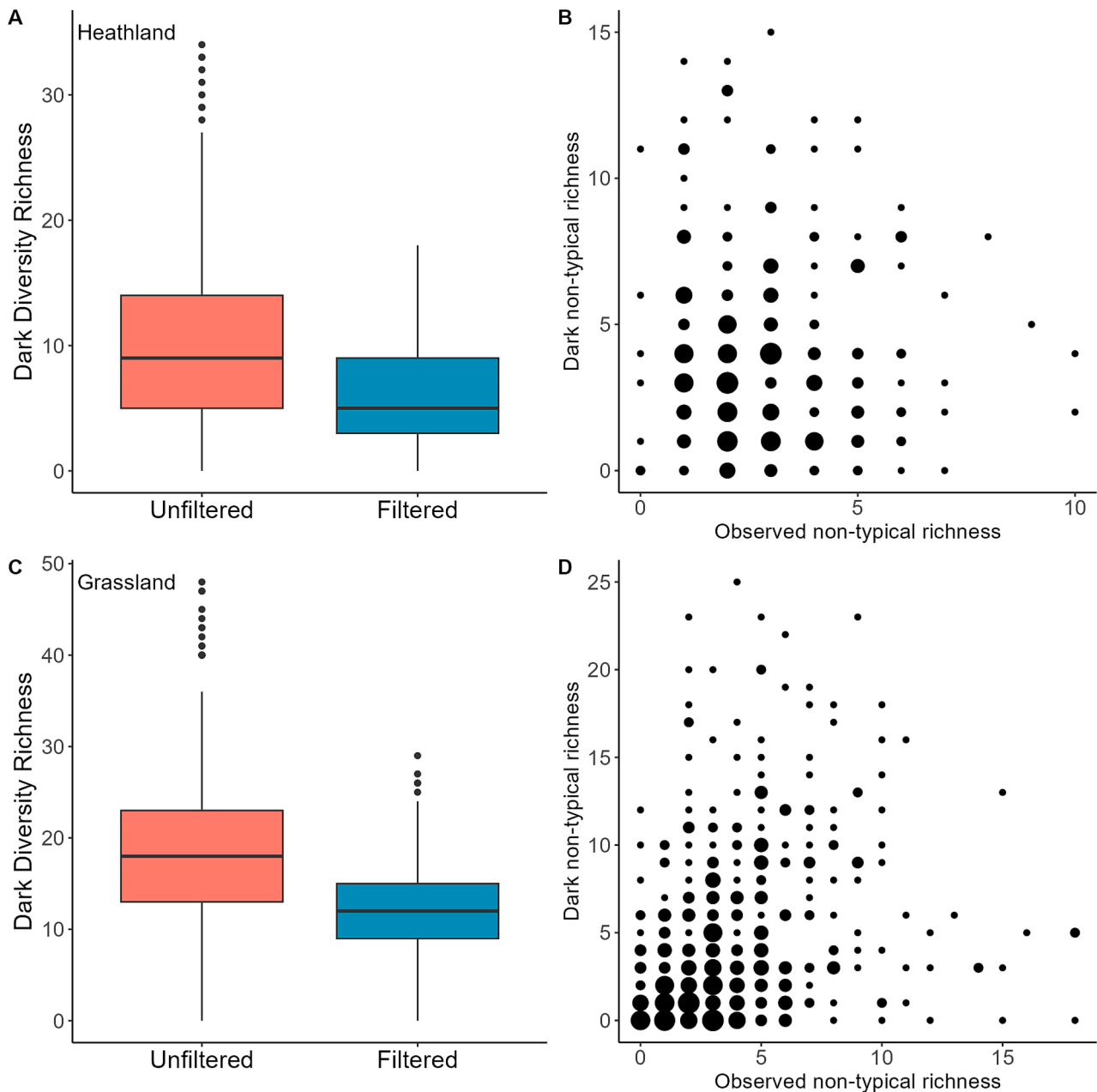


Fig. 3. Species richness in the dark diversity estimated from an unfiltered and a filtered species pool (first column) and relationship between the richness of nontypical species in observed and in dark diversity (second column) in heathland and grassland.

leads to the inclusion of nontypical species in the dark diversity (Fig. 1B). As previously found, dark diversity makes it possible to predict the species currently in colonisation credit, i.e., species yet to colonize a patch, but which will according to their characteristics (Gijbels et al. 2012; Belinchón et al. 2020). However, if the species in colonisation credit are nontypical species, the conclusions we draw will be the opposite of what we are looking for. Species may be in colonisation credit for very different reasons, each reflecting a possible community change towards a more degraded state or, on the contrary, towards an improved state. By filtering out species in colonization credit that belong to the habitat-specific pool, our method can therefore help practitioners to shed light on the successful restoration trajectories that can be achieved.

4.2. Advantages of restricting to habitat-specific species pool before dark diversity estimation

Our results provide evidence for the need to restrict dark diversity estimates to habitat-specific species pool. Nevertheless, an important question is to determine at which stage this restriction shall be conducted. In fact, there are three possibilities, and although a detailed comparison is beyond the scope of this study, the advantages and disadvantages of each must be mentioned. The first is the one that has been implicitly used up to now in studies on dark diversity (Fløjgaard et al. 2020; Dalle Fratte et al. 2022; Hostens et al. 2023), and consists of making a preliminary selection of the areas to be sampled by selecting only sites in a very good state of conservation and which consequently contain no (or very few) nontypical species. This approach may intuitively seem the most interesting because it does not require species to be classified into typical and nontypical species. However, it can hardly be

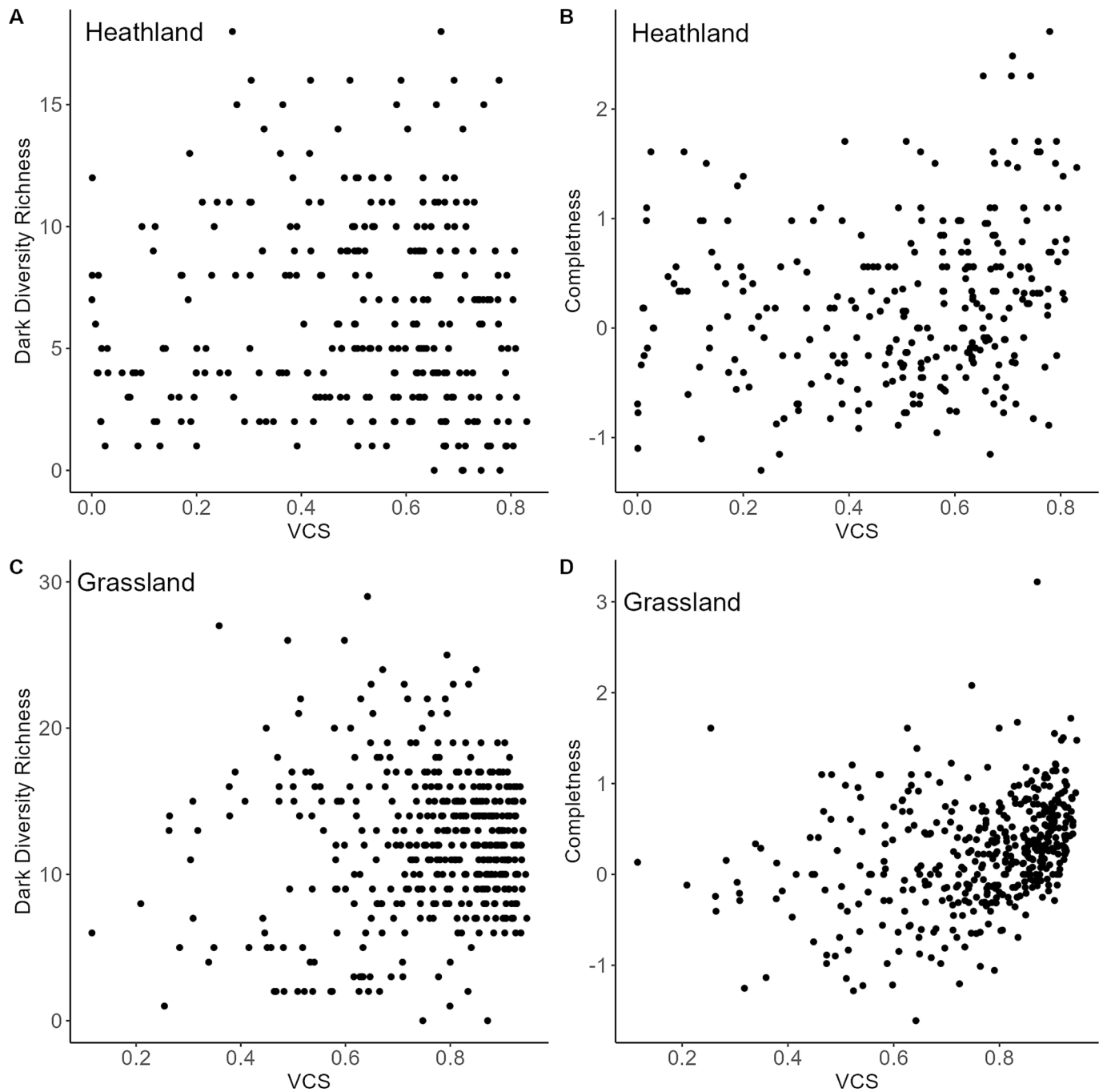


Fig. 4. Relationship between the observed conservation status (VCS) and dark diversity richness and completeness in heathland and grassland.

applied in a conservation or restoration context, in which degraded sites hosting nontypical species are inevitably included in vegetation datasets. In the context of conservation or restoration, it is therefore necessary to classify species according to their membership of the habitat's specific pool. However, there are two ways of restricting the estimation of dark diversity. In the approach proposed here, we restricted the habitat-specific pool before estimating dark diversity, i.e. to exclude nontypical species from the cooccurrence matrices used for the estimates. However, another approach could be to carry out this restriction a posteriori, i.e. to remove nontypical species from the dark diversity after having made the dark diversity estimates. Although the results provided by the two restriction methods are quite similar in our case, the two possibilities offer advantages and disadvantages that are important to mention. The main advantage of the method we chose is that only

cooccurrences between typical species are taken into account in the estimates of dark diversity, thus avoiding the inclusion of typical species due to their frequent cooccurrence with nontypical species. It should be noted, however, that the a posteriori approach has the advantage of allowing to study the nontypical species in the dark diversity as a metric reflecting the potential future habitat degradation. In fact, if two sites with the same observed conservation status have a large number of predicted nontypical species on one site but not on the other, it is likely that the former has a greater risk of future degradation than the latter. Further studies will be needed to better understand in which context one of the two approaches is more relevant than the other.

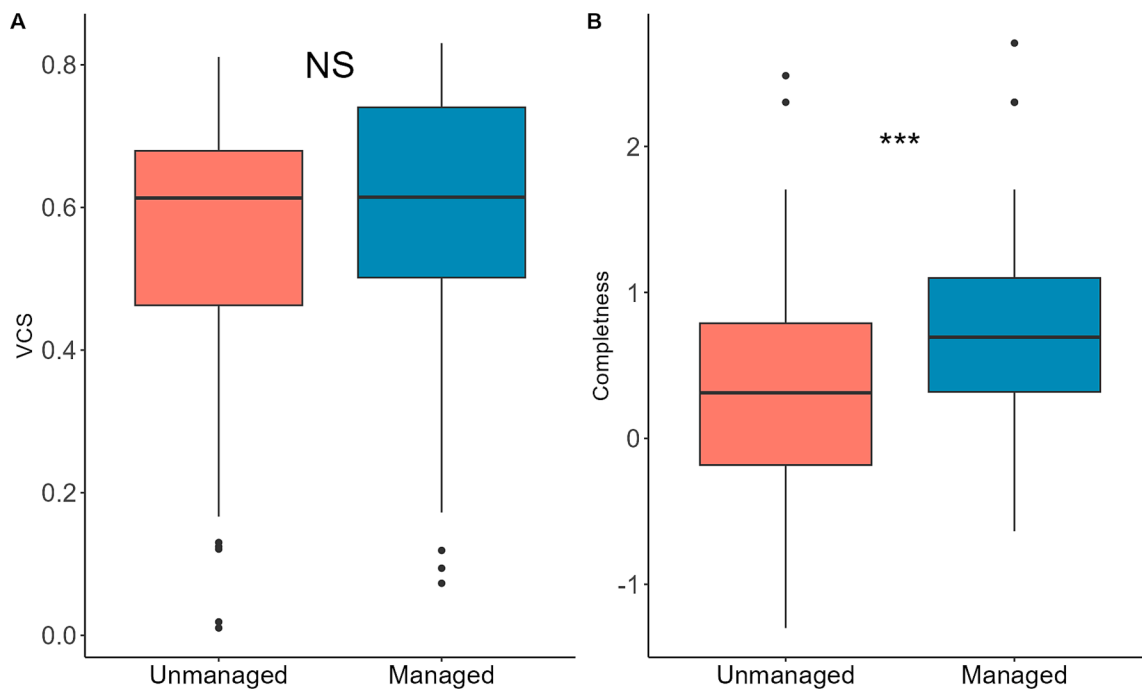


Fig. 5. Box plot of habitat conservation status (VCS index) and completeness between unmanaged and managed heathlands in the Canut protected area. * indicate significant difference tested with Wilcoxon rank test.

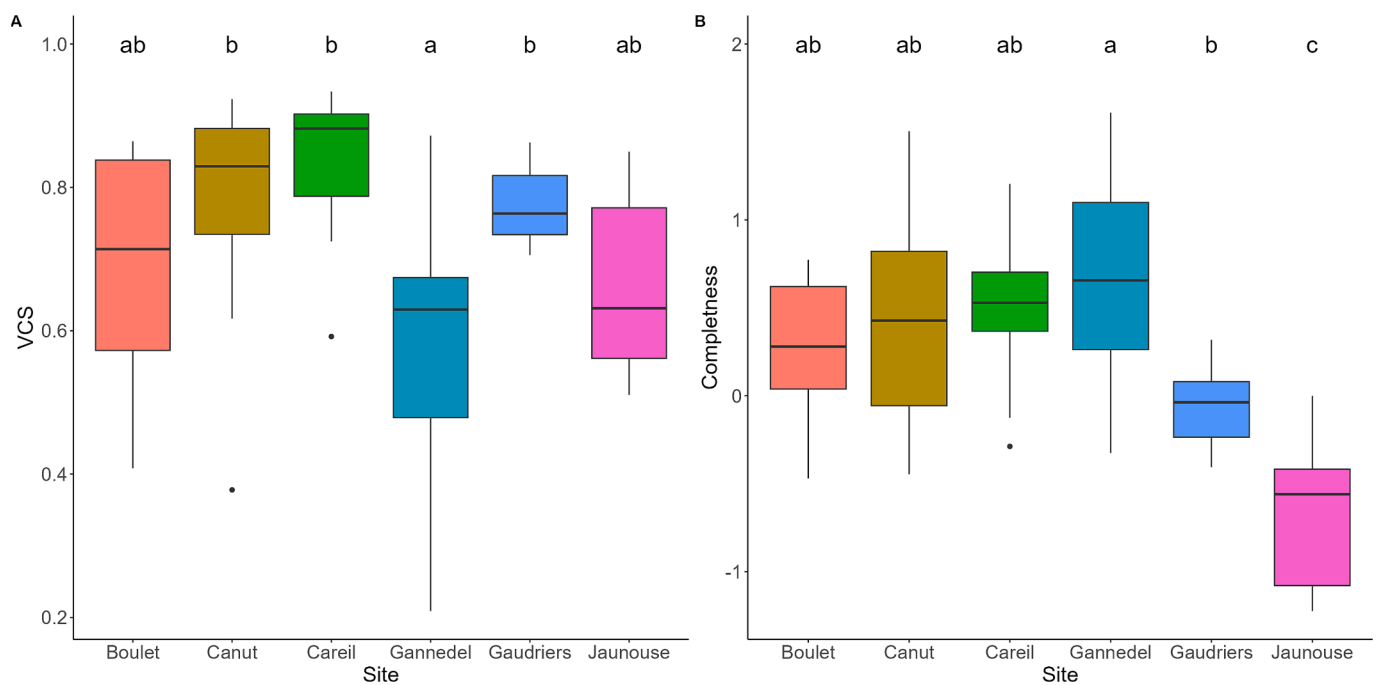


Fig. 6. Box plot of habitat conservation status (VCS index) and completeness of grasslands in six protected areas. Letters indicate significant differences among site tests with a pairwise Wilcoxon post hoc test with Bonferroni correction.

4.3. Complementarity between habitat conservation status and dark diversity

In the two habitats studied, we have shown that observed conservation status and dark diversity are not only nonredundant (Fig. 4), but also complementary (Figs. 5 & 6). They can therefore be used jointly to prioritise the conservation or restoration of sites and assess the effectiveness of management.

In order to prioritise the need for management or restoration of sites,

the combination of conservation status and dark diversity metrics makes it possible to distinguish four situations that we observed in our grassland case study. Firstly, sites whose conservation is a priority, such as the Canut and Careil sites, because they have a good observed conservation status (i.e. high VCS or FCS_i) and a high level of completeness (or a low dark diversity richness). Second, sites that present significant management challenges, such as the Jaunouse and Gaudrier, which, despite their favorable conservation status, have low completeness, indicating that management measures could further improve their conservation

status. Third, sites with an unfavourable conservation status (i.e. low VCS or FCS_i) but high completeness, which therefore would not gain much from management or restoration operations. In our study case, this situation appears for Gannedel, a particular site due to its location in a naturally eutrophic wetland, leading to an original plant community compared with other grasslands in the region, but which is naturally species-poor. Fourth, sites with both a low observed conservation status and low completeness, which can probably only be improved by important restoration measures, but which have great potential due to their high dark diversity richness. In this study case in six protected areas, prioritisation of management and/or restoration operations solely based on the observed conservation status would indicate that the Gannedel site hosts the grasslands with the greatest need, as they have the lowest VCS values. However, when the missing part of the diversity is included, a complementary message emerges. The regionally original grasslands at the Gannedel site present a very high completeness and will probably not be greatly improved by management/restoration operations. However, the grasslands at the Jaunouse and Gaudriers sites, although they are already in an interesting state of conservation, have considerable room for improvement and should therefore be given priority.

Similarly, in the heathland case study of the Canut Valley protected area, our results indicate the complementarity of observed and dark diversity metrics. In fact, the lack of effectiveness of management we found when using the metrics of observed conservation status (i.e., VCS and FCS_i) is contradicted by the dark diversity metrics which indicate a positive effect of management. Therefore, our results indicate a complementarity in the information provided by observed diversity and dark diversity, which can help conservation practitioners assess the effects of management measures.

4.4. Implications for management

This research is the first to confirm the complementarity of observed habitat conservation status and dark diversity in heathland and grassland habitats. This complementarity offers avenue for improving existing conservation strategies as the absence of species from a site provides information that can help practitioners prioritize sites for conservation or restoration and to evaluate the management/restoration operations implemented. However, our results also show that estimates of dark diversity must be restricted to species belonging to the habitat's specific pool. Otherwise, a large proportion of the dark diversity will be made up of nontypical species, leading to an increase in richness and bias in the proposed diagnosis and prioritisation. The method proposed here has the advantage of being simple and easy for practitioners to implement, particularly given the availability of a platform to calculate both dark diversity (<https://shiny.botany.ut.ee/DarkDiv/>) and conservation status (<https://outils.ecobio.univ-rennes.fr/paysabio/vcs/>).

CRediT authorship contribution statement

Simon Chollet: Writing – original draft, Investigation, Formal analysis, Conceptualization. **Mathilde Dano:** Writing – review & editing, Investigation, Formal analysis. **Gabrielle Thiébaud:** Writing – review & editing. **Vincent Jung:** Writing – original draft, Investigation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.112990>.

Data availability

Data will be made available on request.

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