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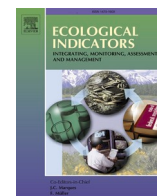
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## Integrating species pools and abundance distribution in habitat conservation status assessment: A new index

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### ABSTRACT

Habitat degradation and fragmentation are recognized as major causes of biodiversity loss, and effective management to conserve habitats is highly dependent on our ability to assess their conservation status. In this study we introduce a new index (VCS, for vegetation conservation status) to assess the conservation status of plant communities, which reflect the identity of habitat types. The VCS index is based on the same probabilistic approach than the classical Simpson's diversity index, but uses the concept of species pools to integrate the influence of 'typical' and 'non-typical' species on habitat conservation status. In addition to the effect of species identity, this index also allows the detection of change in conservation status because of variation in species-abundance distribution. As an example we applied the VCS index to two heathland habitats in French Brittany and we compared the values provided by the index to qualitative assessments by heathland experts. We also compared the performance of the VCS index against three other indices: species richness, species diversity and a more recent index of 'favourable conservation status'. Among the four indices tested, the VCS index was the most effective in assessing the vegetation conservation status when compared against qualitative assessment by heathland experts. Moreover the VCS index, coupled with variance partitioning methods, allowed to quantify the contribution of expected causes of habitat degradation. This study demonstrates that the use of habitat-specific species pools to distinguish between typical and non-typical species, as well as the consideration of species abundances, are critical for an accurate assessment of the vegetation conservation status. The VCS index should therefore be a valuable tool for both managers and researchers involved in habitat conservation.

### 1. Introduction

Human-induced changes such as direct habitat degradations, land use changes or biological invasions have led to the depletion of many habitats and to the designation of sites for their conservation (Ostermann, 1998). In this context, effective habitat conservation requires to determine where management actions are needed and to evaluate their efficiency. In most cases habitat types are mainly defined on the basis of their vegetation composition. Managers seeking to maintain or restore habitats must therefore be able to objectively assess the conservation status of vegetation, i.e. its 'quality' relative to that expected under optimal conditions.

A first approach to evaluate the conservation status of vegetation is to use 'classical' biodiversity indices such as species richness (i.e. the

number of species present in a given plant community) or species diversity (e.g. Shannon or Simpson indices) that take into account both the species richness and the distribution of abundances among species (species evenness). Although sometimes used by scientists (Yoccoz et al., 2001; Sluis, 2002; Cantarello and Newton, 2008; Lukács et al., 2013) and by protected area managers, this approach may not be appropriate as a high species richness (or diversity) is not always a good indicator of a favourable conservation status (Lamb et al., 2009; Filippi-Codaccioni et al., 2010). A loss of species due to habitat degradation can indeed be compensated by the colonization by other species. Moreover, resident species can persist due to an extinction debt, therefore resulting in a higher species richness in degraded than in non-degraded habitats (Jackson and Sax, 2010).

The conservation status of vegetation can also be evaluated by using

Abbreviation: VCS, vegetation conservation status.

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some indicator species (Carignan and Villard, 2002; Siddig et al., 2016; Silva et al., 2019), which can include habitat-specialist species (e.g. wetland species, Yepsen et al., 2014), rare endangered species or species related to habitat degradation (e.g. ruderal species, Vécrin and Muller, 2003). The detection of indicator species can be integrated in multi-criteria evaluation grids with other habitat parameters defined by regional experts (Maciejewski et al., 2015). A practical interest of this approach is that the vegetation conservation status can be easily assessed from a reduced species list and does not require a strong botanical knowledge of the habitat under scrutiny. However, in addition to habitat-specialist species, plant communities also contain many generalist species that are an important part of community and should be taken into account while providing an integrative assessment of the vegetation conservation status.

Floristic quality assessment (FQA) measures have been developed in North America to quantify the conservation status of vegetation (Swink and Wilhelm, 1994; Freyman et al., 2016). They are based on an expert evaluation of species' affinity to more or less human-impacted habitats and are widely used in North America, where landscapes with very low human pressure still exist. However, FQA measures are difficult to apply in European countries, where most habitats of high conservation interest have a long history of human impact (Landi and Chiarucci, 2010).

Recent approaches consist in analysing the species composition of a given plant community in comparison with the habitat-specific species pool (Pärtel et al., 1996; Zobel et al., 1998; Zobel, 2016). A habitat-specific species pool (or filtered pool, Cornell and Harrison, 2014) corresponds to the set of all species in a region that can potentially inhabit a site because of suitable ecological conditions (Fig. 1). From a conservation perspective, it can be defined as a list of potential 'typical species' that belong to the plant species composition expected under the absence of habitat degradation. This corresponds to habitat-specialist species, but also includes generalist species often co-occurring as well as rare

species (Dupré, 2000; Helm et al., 2015). For example, in heathland habitats, habitat-specific species pool would include habitat specialist species like *Erica* sp., but also more generalist species such as *Molinia caerulea* or very rare species such as *Gladiolus illyricus* (Chambers et al., 1999; Kleijn et al., 2008; Mobaied et al., 2011; Glemarec et al., 2015). Species belonging to such habitat-specific species pool could also be targeted as 'typical species' for conservation and restoration, as they represent the ecologically relevant set of species for that habitat. In contrast, observed species that do not belong to the habitat-specific species pool can be defined as 'non-typical species' (Fig. 1). These species comprise non-native species or any species related to strong human perturbation (e.g. ruderal species), but can also include species reflecting natural ecological succession, especially for habitats historically created and maintained by traditional management practices (e.g. calcareous grasslands, wet meadows, heathlands, Ostermann, 1998; Halada et al., 2011). In heathland habitats for example, the colonization by shrub and tree species due to the abandonment of traditional management is recognized as a main cause of decline at the European scale (Webb, 1998; Fagúndez, 2013).

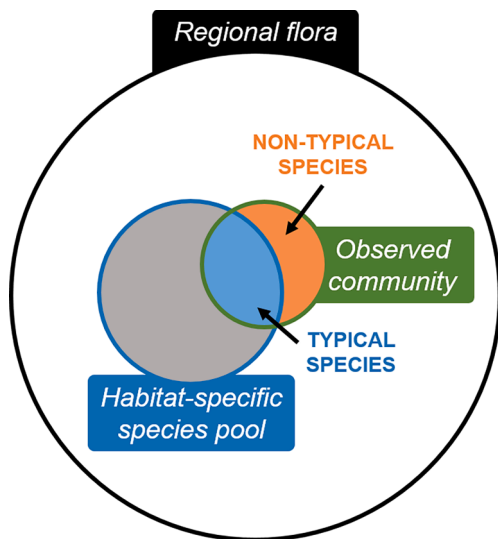
In order to evaluate the conservation status of a particular habitat, Helm et al. (2015) proposed an 'index of favourable conservation status' (FCS<sub>i</sub>), formulated as the log ratio of typical species richness (named 'characteristic diversity' in Helm et al. (2015)) to non-typical species richness (named 'derived diversity' in Helm et al. (2015)). Compared to other classical indices such as species richness or species diversity, the FCS<sub>i</sub> index is highly relevant because it takes into account the positive and negative influences of typical and non-typical species, respectively, in assessing vegetation conservation status. However, this index does not take into account the abundance of species within the observed plant community, which is an important component of its conservation status. Indeed, managers may consider a given community to be in an unfavourable conservation status if it is dominated by non-typical species (e.g., a heathland with an important tree cover), regardless of the number of these species. The conservation status can also be affected by the abundance distribution within the typical species (Muñoz-Barcia et al., 2019). For example, in heathlands, typical species such as *Ulex europaeus* can become locally hyper-abundant and decrease the abundance of low-stature species (Rees and Hill, 2001). In summary, we consider that the conservation status of a given plant community can be degraded as a result of three distinct causes: (1) a decrease in the richness of the typical species, (2) an increase in the abundance of the non-typical species and (3) a strong dominance of one typical species over the others. To our knowledge, no methods have been proposed to quantify the vegetation conservation status by taking into account both of these potential causes of degradation.

The well-known Simpson diversity index measures species diversity as the probability that two randomly sampled individuals within a community belong to different species. Here we propose a new index of vegetation conservation status based on the same probabilistic approach but which integrates the influence of typical and non-typical species. To demonstrate the potential of our index, we applied it to a vegetation dataset collected in heathland habitats, which are of high conservation interest in the Atlantic biogeographic region (Council Directive 92/43/EEC; European Commission, 1992). Then, we compared qualitative assessments of vegetation conservation status made by heathland experts to results produced by our index, by the FCS<sub>i</sub> index (Helm et al., 2015) and by two classical biodiversity indices (species richness and species diversity). Finally, we evaluated the relative contribution of expected causes of degradation on the vegetation conservation status.

## 2. Materials and methods

### 2.1. Index of vegetation conservation status

We proposed a method to evaluate the vegetation conservation status by modifying the Simpson's diversity index (Simpson, 1949) or Gini



**Fig. 1.** Conceptual diagram illustrating the typical and non-typical species pools used to evaluate the vegetation conservation status of an observed community. The regional flora (large black circle) corresponds to all species occurring in a particular biogeographic region that encompasses different ecological conditions. The habitat-specific species pool (blue circle) corresponds to the set of all species that can potentially inhabit particular ecological conditions. The observed community (green circle) represent species recorded at a given location. The blue area illustrates the typical species (i.e. the observed species that belong to the habitat-specific species pool) and the orange area the non-typical species (i.e. the observed species that do not belong to the habitat-specific species pool). Note that the grey area corresponds to the absent part of the habitat-specific species pool, i.e. the dark diversity (Pärtel et al., 2011).

coefficient:

$$D = 1 - \sum \left( \frac{n_i}{N} \right)^2 \quad (1)$$

where  $n_i$  is the abundance of each species  $i$  and  $N$  the sum of the abundance of all species. For plant communities, as the index is usually applied to cover abundance data and not to numbers of individuals, there is no need to adjust this formula to prevent bias due to finite sample (Bennie et al., 2011). The Simpson's diversity index ranges from 0 to 1 and represents the probability that two randomly chosen points within the sample area are occupied by different species. It accounts for both the number of species present in the community (species richness) and the distribution of abundances among species (species evenness).

We modified the Simpson's diversity index to include the distinction between typical and non-typical species and to propose a new index of vegetation conservation status (VCS). We considered that a plant community has a high conservation status if it satisfies three criteria, in accordance with the three potential causes of degradation described previously. The first criterion is that the plant community has a high typical species richness. The second criterion is that no particular typical species strongly dominate the others. The third criterion is that the plant community has a low abundance of non-typical species. Similar to the Simpson's probabilistic approach, the evaluation of these three criteria is equivalent to determining the probability that two randomly chosen points within the sample area are occupied by different typical species. The VCS index therefore corresponds to this probability, which is formulated as:

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

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 non-typical species. We provide in [Supplementary material \(Appendix S1\)](#) the formula that should be used with individual counts instead of cover abundance data (e.g. for animal communities), as well as the R script to calculate the VCS index for both formulas ([Appendix S2](#)). The VCS index varies from 0 to 1 and is maximized if there are many typical species with equally distributed abundances ([Fig. 2a](#)) and if there is a low abundance of non-typical species ([Fig. 2b](#)). When the abundance of the non-typical species

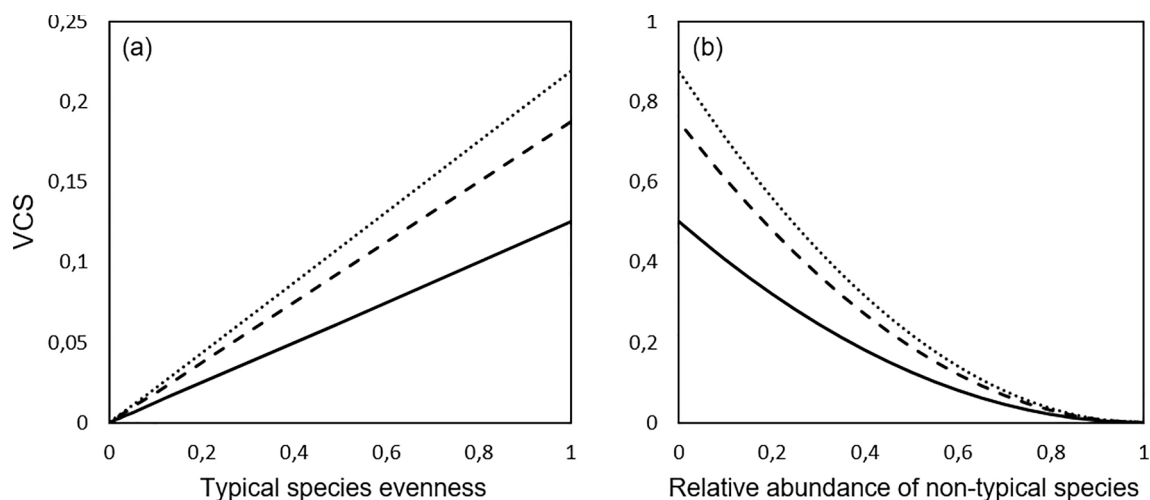
decreases in favour of the typical species, the VCS index obviously converges to the Simpson's diversity index.

## 2.2. Case study: French Brittany heathlands

We applied the VCS index in heathland habitats located in French Brittany. This region has a large area covered by heathlands and thus has a high responsibility for their conservation (Gloaguen, 1984; Glemarec et al., 2015). As for the rest of the Atlantic part of Western Europe, the high abundance of heathlands in Brittany results from the combination of past agricultural practices such as grazing, cutting and burning on sites with acidic soil (Webb, 1998). However, the decline of these practices has led to the natural colonization by tree species (Mitchell et al., 1997) and the overdevelopment of competing species such as *Molinia caerulea* or *Pteridium aquilinum* (Pakeman and Marris, 1992).

Heathlands were sampled in two protected areas ('Vallée du Canut' and 'Chambre au Loup') representing the heathland landscapes of inland Brittany and comprised two main types of habitats depending on soil moisture conditions: dry heathlands and mesic heathlands. The dry heathlands are located at high topographic positions on shallow soils with locally exposed bedrock, which generates a vegetation mosaic of shrubs (*Erica cinerea*, *Calluna vulgaris*, *Ulex europaeus*) that alternate with xerophytic grassland patches (Glemarec et al., 2015). The mesic heathlands are generally located on deeper soils at lower topographic positions and are dominated by dwarf shrubs (*Erica ciliaris*, *Calluna vulgaris*, *Ulex minor*) and by *Molinia caerulea*. About one-third of the surface of each protected area benefits from conservation management that aims to maintain heathland habitats by removing tree species. The unmanaged locations (no management for at least 30 years) have been historically occupied by open heathlands and are now more or less colonized by forest tree species.

The species composition of the vegetation was recorded by means of 40 plots (4 m × 4 m) in each heathland type (dry and mesic). For the dry heathland, all plots were located in the site 'Vallée du Canut' as the other site is mainly covered by mesic heathlands. For the mesic heathland, plots were equally distributed between the two sites (20 plots per site). Plots within a site were randomly distributed to encompass the full range of successional stages. The distance between each plot varied from 30 m to 2000 m. We recorded all vascular plants within each field plot and we estimated their cover using the Braun-Blanquet scale (transformed to mean percentage cover class for data analysis).



**Fig. 2.** Results obtained from simulated data do describe the response of the vegetation conservation status (VCS) index to changes in typical species richness, typical species evenness and relative abundance of non-typical species. The graph (a) represents the effects of typical species evenness (Simpson's evenness) on the VCS index according to three levels of typical species richness (solid, dashed and dotted lines for 2, 4 and 8 typical species, respectively), by maintaining the relative abundance of non-typical species at a constant level of 0.5. The graph (b) represents the effect of the relative abundance of non-typical species on the VCS index according to three levels of typical species richness, by maintaining constant the typical species evenness (abundance equally distributed among typical species).

### 2.3. Determination of the typical species

In order to determine the typical species in the sampled heathlands, we used the French interpretation manuals of European Union habitats (Bensettiti et al., 2005). In these manuals, each EU habitat is declined into elementary habitats occurring in different geographical locations, with an indicator species list resulting from a synthesis of historical phytosociological studies. We therefore used the advantage of having well described habitats and available lists of typical species defined by regional experts (Clément and Touffet, 1978; Gloaguen, 1984). Importantly, these species lists are not restricted to the habitat-specialist species and also indicate generalist and rare species. We considered different habitats belonging to the ‘European dry heathlands’ (habitat code 4030) including the dry heathlands *sensu stricto* (elementary habitats 4030-6 and 4030-7 in the French interpretation manual) and the mesic heathlands (elementary habitat 4030-8). We also considered the acidic grasslands of rocky outcrops (elementary habitats 6230-7 and 8230-5) to take into account the grassland patches often included in the dry heathlands.

Among the 54 species recorded in the field, 19 species were identified as typical species of the dry heathland, 10 species as typical species of the mesic heathland and 31 as non-typical species (Appendix S3). The non-typical species were mainly forest species, grassland species and bracken *Pteridium aquilinum*. We acknowledge that bracken could have been assigned to typical species, as heathlands with bracken can be recognized as a subtype of mesic heathland (Gloaguen, 1984; Glemarec et al., 2015). We decided to consider bracken as non-typical because (1) it is not listed as indicator species in the manual of EU habitats where it is instead mentioned as revealing habitat degradation (Bensettiti et al., 2005) and (2) most of the management (and restoration) actions carried out in the Brittany mesic heathlands focus on the limitation of bracken. However, we provide in Appendix S4 all the results from the data analyses with bracken considered as typical species.

### 2.4. Expert participation

We calculated the VCS index for each of the 80 field plots. In order to confirm that the index reflects the perception of conservation practitioners, we compared the evaluation of conservation status based on the index to qualitative assessments by heathland experts. We sent parts of our vegetation dataset to 25 regional experts, belonging to 14 independent institutions. All experts have been actively involved in heathland conservation for many years and have in-depth field knowledge of these habitats. They are managers of natural areas dominated by heathlands for 76% of them and botanical experts for 24% of them. Each participant received data from 12 vegetation plots (six from the dry heathland, six from the mesic heathland) randomly selected within our 80-plots dataset. We asked experts to score each plot as ‘favourable’, ‘intermediate’ or ‘unfavourable’ solely on the basis of its plant species composition (species names with Braun-Blanquet cover-abundance values), without any indication about our typical species list and our VCS index. We also asked participants to self-assess their botanical knowledge by indicating the number of species they knew. Sixty percent of them stated that they knew all the species listed and 40% knew at least 80% of the species.

### 2.5. Data analysis

To evaluate the congruence between VCS values and expert categorical scores, we used a linear mixed-model with the VCS index as response variable, the expert score as fixed effect and the identity of expert as random effect. For the mesic heathland, as plots came from two different sites, we also included the site as random effect. We repeated the same analysis by using either the species richness, the species diversity (Simpson’s diversity index) or the index of favourable conservation status ( $FCS_i = \log(\text{typical species richness}/\text{non-typical species$

richness)) proposed by Helm et al. (2015) as response variable. For each response variable, we used the marginal  $R^2$  (variance explained by the fixed effect only) to determine the amount of variance explained by expert score (Nakagawa and Schielzeth, 2013). To test for spatial autocorrelation we used the residuals of each model to draw spline correlogram plots with 1000 permutations in the ncf package in R (Bjornstad, 2020). No sign of autocorrelation was found in any model (Appendix S5).

For each heathland type, we determined the proportion of variance of VCS explained independently by each of its three basic components, i. e., typical species richness, typical species evenness and relative abundance of non-typical species using a hierarchical partitioning approach (Chevan and Sutherland, 1991). We performed the same analysis in order to explain variation in VCS by more specific causes of heathland degradation. We used as explanatory variables the relative abundance of the non-typical species *Pteridium aquilinum* or species groups (forest species and grassland species) known to reflect degradation of heathland communities (Watt, 1955; Pakeman and Marrs, 1992; Fagúndez, 2013). We also included the relative abundance of two typical species (*Ulex europaeus* and *Molinia caerulea*) known to potentially dominate other typical species and therefore reduce evenness (Heil and Bruggink, 1987; Marrs et al., 2004).

## 3. Results

The VCS index varied from 0.01 to 0.76 in the dry heathland and from 0 to 0.78 in the mesic heathland. We provide different examples of observed plant species composition related to low and high value of VCS in Appendix S6. The VCS values equal or close to zero correspond to highly degraded plots that no longer contain typical species, and which obviously can no longer be considered as heathland habitats.

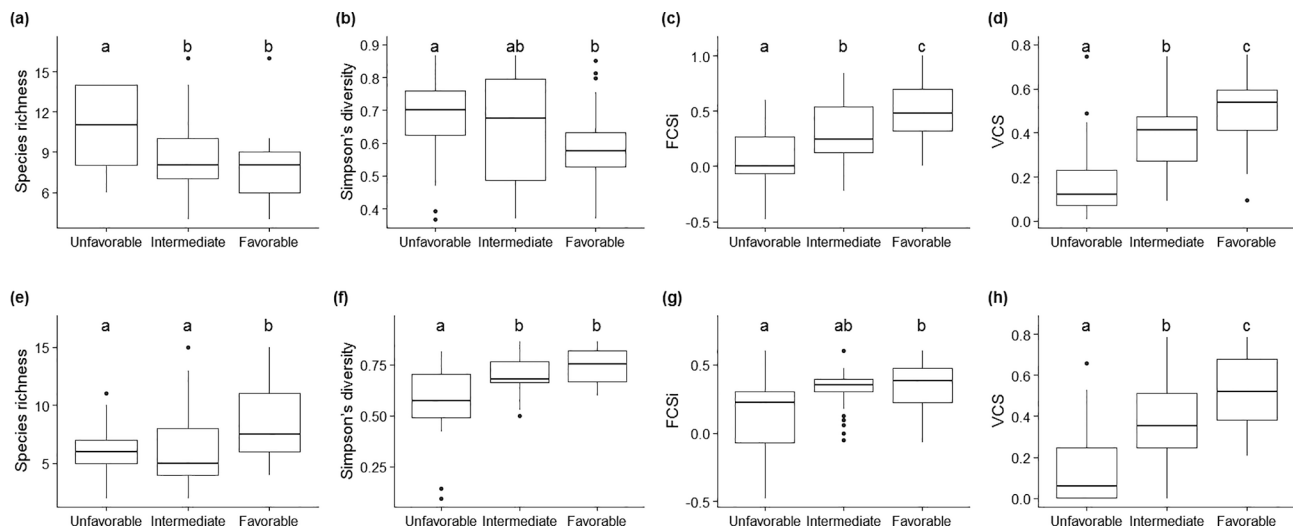
Compared to the other indices (species richness, Simpson’s diversity and  $FCS_i$ ), the VCS index was the only one that varied significantly among the three expert scores for both the dry and the mesic heathland (Fig. 3). For the dry heathland, species richness and species diversity varied significantly among expert scores (Fig. 3a, b), but both indices were higher in plots scored as ‘unfavourable’ than in plots scored as ‘favourable’. Moreover, the proportion of variance explained by expert scores (marginal  $R^2$ ) was higher for VCS (43% and 46% for the dry and mesic heathland, respectively) than for species richness (19% and 12%), Simpson’s diversity (9% and 25%) and  $FCS_i$  (30% and 18%).

Among the three basic components of VCS, the relative abundance of non-typical species was the main contributor to the differences in VCS values, followed by typical species evenness and then by typical species richness (Table 1). For the dry heathland, the effect of typical species richness was not statistically significant. The contribution of particular species or species groups differed between the dry and the mesic heathland (Table 2). For the dry heathland, VCS was mainly decreased by the abundance of forest species, followed by the abundance of grassland species. For the mesic heathland, VCS was mainly decreased by the abundance of *Pteridium aquilinum*, followed by the abundance of forest species.

## 4. Discussion

### 4.1. VCS versus other indices

Among the four indices tested (species richness, Simpson’s diversity,  $FCS_i$  and VCS), the VCS index was the most congruent with the qualitative assessment of conservation status by heathland experts. As expected, species richness and species diversity were not consistent with expert scores. Interestingly, for the dry heathland, plots with high species richness and diversity were rated as ‘unfavourable’. This can be explained by the fact that in plots with a high species richness, the presence of non-typical species (considered negatively by experts) is not compensated by a loss of typical species. More specifically, in most plots



**Fig. 3.** Variation in different indices (species richness, Simpson's diversity, FCS<sub>i</sub> and VCS) between qualitative assessments of vegetation conservation status by experts, for the dry heathland (a–d) and for the mesic heathland (e–h). Significant differences ( $P < 0.05$ ) evaluated by Tukey's post-hoc tests are indicated by different letters.

**Table 1**

Hierarchical variance partitioning of the VCS index into its three basic components (typical species richness, typical species evenness and relative abundance of non-typical species) for the dry and the mesic heathland. For each explanatory variable, the percentage of explained variance is indicated, as well as the direction of the effect (arrow). Significant effects are indicated by asterisks (\*\* $P < 0.001$ , \* $P < 0.01$ , \* $P < 0.05$ ). Bottom line (total  $R^2$ ) indicates the total variance of VCS explained by the three explanatory variables.

|   |   | Dry heathland | Mesic heathland |
|---|---|---------------|-----------------|
| Typical species richness                  | ↑ | 7             | 17*             |
| Typical species evenness                  | ↑ | 20***         | 18**            |
| Relative abundance of non-typical species | ↓ | 73***         | 65***           |
| Total $R^2$                               |   | 0.90          | 0.87            |

**Table 2**

Hierarchical variance partitioning of the VCS index into expected causes of heathland degradation (relative abundance of forest species, grassland species, *Pteridium aquilinum*, *Ulex europaeus*, and *Molinia caerulea*) for the dry and the mesic heathland. For each explanatory variable, the percentage of explained variance is indicated, as well as the direction of the effect (arrow). Significant effects are indicated by asterisks (\*\* $P < 0.001$ ). Bottom line (total  $R^2$ ) indicates the total variance of VCS explained by all explanatory variables.

|                            |   | Dry heathland | Mesic heathland |
|----------------------------|---|---------------|-----------------|
| Forest species             | ↓ | 70***         | 34***           |
| Grassland species          | ↓ | 20***         | 1               |
| <i>Pteridium aquilinum</i> | ↓ | 3             | 57***           |
| <i>Ulex europaeus</i>      | ↓ | 7             | 7               |
| <i>Molinia caerulea</i>    | ↓ | <1            | 1               |
| Total $R^2$                |   | 0.64          | 0.77            |

dominated by non-typical forest species, typical species such as *Erica cinerea*, *Calluna vulgaris*, *Ulex europaeus* or *Agrostis curtisii* remain, albeit in low abundance (Appendix S6). These results confirm that species richness and diversity are not suitable for evaluating vegetation conservation status (Lamb et al., 2009). This is particularly the case for species-poor habitats such as heathlands, where high species richness can be viewed as a sign of degradation.

The FCS<sub>i</sub> index, although based on the distinction between typical and non-typical species, also proved to be less effective than the VCS index in discriminating expert scores. A main difference between these two indices is that VCS takes into account the abundance of species

while FCS<sub>i</sub> does not, which lead to different assessments of the conservation status. For example, for the mesic heathland, FCS<sub>i</sub> did not vary between the plots scored as 'intermediate' by experts and the plots scored as 'unfavourable', whereas VCS differed significantly. The explanation for this result is that the two categories of plots differed mainly in the abundance rather than in the number of non-typical species. This demonstrates that experts attach great importance to the abundance of non-typical species, which cannot be overlooked when assessing vegetation conservation status. The VCS index, by taking into account the abundance of non-typical species, thus provides an assessment of the vegetation conservation status that is consistent with that of experts.

#### 4.2. Properties of the VCS index

The VCS index has similar properties to the Simpson's diversity index from which it is derived. In particular, the VCS index gives more weight to abundant species than to rare species and does not take into account species conservation priorities. Thus, it cannot substitute for monitoring of particular rare endangered species whose presence may, however, be decisive for managers to declare a favourable conservation status. In fact, the evaluation of the conservation status based on the whole species composition or on particular species can be seen as complementary approaches, which do not necessarily lead to the same decisions. For example, the typical endangered species *Gladiolus illyricus* was recorded in four plots of the dry heathland (with VCS ranging from 0.19 to 0.58) and was not recorded in plots with the highest VCS values.

Another important feature of the VCS index is that, although it is mathematically bounded between 0 and 1, the maximum value it can actually reach depends on the level of species richness of the habitat under consideration and will tend to be higher for species-rich than for species-poor habitats. Thus, as other diversity indices, VCS should be used to compare communities that belong to the same target habitat, but is not suitable to compare different habitats (e.g. heathland vs. species-rich grassland). Moreover, even at a given level of typical species richness, it is unlikely that VCS can reach its maximum value assuming equal abundance among typical species. Indeed, although some typical species may become overabundant, an equal abundance among typical species is unrealistic as both dominant and subordinate species usually occur in most habitats. The threshold VCS value above which a plant community can be considered to be in a favourable conservation status is highly dependent on the habitat type and can be defined from vegetation data

collected in reference locations.

#### 4.3. Identification of typical and non-typical species

The main challenge in using the VCS index is to identify, among the recorded species, which should be assigned to typical species and which should be assigned to non-typical species. In this study, the identification of the typical species was made possible through the use of the French interpretation manuals of European Union habitats (Bensettiti et al., 2005). The declination of the EU habitats into elementary habitats according to regional specificities – and the associated indicator species lists – is a major asset and allowed us to easily identify the species belonging to the habitat-specific pool within our study region. It would be of great interest if such comprehensive species lists defining species pools of elementary habitats were available to conservation practitioners in all EU countries. Historical phytosociological surveys carried out by regional experts are highly valuable tools for habitat conservation (Dupré, 2000) and can be used to compile regional species lists for EU habitats. Where such historical knowledge is lacking, other methods have been proposed to define habitat-specific species pools, including species distribution models (Guisan and Thuiller, 2005), species ecological requirements (Pärtel et al., 1996), species co-occurrences (Lewis et al., 2016) and ordination analyses (Brown et al., 2019). Helm et al. (2015) developed a standardised multi-step procedure that integrates these different methods and can be recommended to identify typical species in any habitat type.

An important point to raise is that the use of the VCS index does not necessarily imply that all recorded species should be assigned to either typical or non-typical species. Indeed, there may be cases where this assignment is not easy, e.g. for species with a low occurrence rate, or in little-known habitats for which not all specific species have been clearly identified. In such cases, we propose that these species be considered neutral (i.e. neither typical nor non-typical) and therefore not included in the calculation of the VCS index. We also point out that in this study, we did not distinguish between specialist and generalist species among the typical species, as we sought to provide an integrative assessment of the vegetation conservation status. However, such a distinction may be useful, as habitat degradations are expected to affect specialist species more than generalist species, leading to biotic homogenization between different habitats (Rooney et al., 2004; Devictor et al., 2008). Therefore it can be argued that a given community is in favourable conservation status if it is occupied by specialist rather than generalist species. A way to calculate the VCS index with an emphasis on specialist species would also be to consider generalist typical species as neutral, so that they do not influence the index either positively or negatively.

#### 4.4. VCS and habitat conservation management

In our case study, the expert qualitative assessment generally matched with the VCS values, which can be considered as an expert validation of the VCS index. However, the variance of the index for each expert score suggests that there are differences in individual perception of conservation status between experts. A main interest of the VCS index is to provide a quantitative, objective and accurate assessment of the vegetation conservation status, based on a prior selection of typical and non-typical species. Moreover, in contrast to qualitative expert assessment, the VCS index can be implemented in statistical analyses to address different conservation issues. Among others, variance partitioning methods can be applied to evaluate the contribution of anthropogenic or successional factors expected to be implied in habitat degradation, thus helping to prioritize management efforts. In our example, the factors contributing to the decline in VCS were consistent with well documented causes of heathland degradation, especially the colonization by forest species or by bracken *Pteridium aquilinum* due to natural succession (Pakeman and Marrs, 1992; Webb, 1998; Fagúndez, 2013). In some of the dry heathland plots the presence of grassland

species, which contribute to the decline in VCS, could be explained by a high soil nitrogen content due to past agricultural practices or atmospheric deposition (Heil and Diemont, 1983; Britton et al., 2001; Fagúndez, 2013).

Many habitats of high conservation interest are undergoing increasing human pressure or, on the contrary, an abandonment of traditional management practices. Beyond our heathland case study, the VCS index could be used for a wide range of habitats (both terrestrial and aquatic) and degradation causes, including land use changes, pollution and biological invasions. From a practical point of view, as long as habitat-specific species pools are well identified locally, the main skill required to apply the VCS index is to be able to carry out vegetation field surveys. This index can thus be easily and inexpensively applied by managers of protected natural areas, where vegetation surveys are part of the usual habitat monitoring methods. Within the Natura 2000 network, we believe that the VCS index could be widely used to monitor habitat conservation status at the site level, thus helping to define management priorities, identify the main causes of habitat degradation and assess the effectiveness of management practices.

#### CRedit authorship contribution statement

**Vincent Jung:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Writing - original draft, Writing - review & editing. **Lois Morel:** Conceptualization, Writing - review & editing. **Sébastien Bonthoux:** Investigation, Writing - review & editing. **Simon Chollet:** Conceptualization, Formal analysis, Investigation, Methodology, Writing - review & editing.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary data

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