Permanent grassland classifications predict agronomic and environmental characteristics well, but not ecological characteristics

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Declaration of interest

None

Colour

Figure 1, Figure 2 and Figure 3 require colour.

Abstract

Permanent grasslands produce highly diverse ecosystem goods and services, which need to be easily assessed by decision makers. Naturalists and agronomists classify grasslands in different ways to predict ecological, agronomic and environmental characteristics of the grasslands. However, few studies have compared the prediction abilities of these different classifications using the same botanical relevés, and none has explored the utility of combining classifications. In this study, we attributed a grassland class from each of three classifications (phytosociological, agronomic and functional) to 250 permanent grasslands in north-eastern France to predict 16 characteristics: nine ecological, three agronomic and four environmental. We used statistical model selection to identify the classification or combination of classifications that best predicted each characteristic. Our results showed great prediction ability of agronomic classification, which created the best models for predicting agronomic (yield) and environmental (management, elevation) characteristics. We also identified a strong prediction ability of combining two or all three classifications to predict seven other grassland characteristics. However, grassland classifications did not predict most of the ecological characteristics well. We can assume that phytosociological classification, despite its mainstream use, predicts grassland characteristics less well than agronomic classification. We recommend combining grassland classifications to improve rapid prediction abilities. This study provides new knowledge useful for developing grassland classifications which meet the needs of agronomists and naturalists.

Key words: phytosociology; agricultural type; functional type; management; biodiversity; typology

1 Introduction

Worldwide, permanent grassland is the main terrestrial ecosystem, covering 26% of the world land area (FAO, 2019) and 28% of UE total utilised agricultural area in 2013 (Eurostat, 2017). Permanent grasslands provide diverse ecosystem goods and services of global importance, such as forage production, species habitat, pollination, water purification, flood prevention and mitigation of global warming through carbon storage (D'Ottavio et al., 2017). Provision of these services is threatened by four main dangers: disappearance of grasslands (cultivation, degradation), underuse (abandonment), agricultural intensification and climate change (Biró et al., 2013; Muller et al., 1998; WallisDeVries et al., 2002; Young et al., 2005).

Conservation of grasslands and associated goods and services requires strong policy, but grasslands differ and do not need equal protection. Indeed, agronomic and ecological services provided by grasslands are complex consequences of management choices, environmental constraints and botanical composition (Dumont et al., 2018; Michaud et al., 2012). Decision-makers need simple tools such as grassland classifications to assess or predict the levels of grassland services provided. At local scales, farmers and agronomists mainly need to predict forage yield and quality, while naturalists are interested in ecological values of grasslands. At regional, national and international scales, policy makers and administrators need to assess trade-offs between economics and the environment, and to design best policies. To solve these issues, naturalists and agronomists have developed different grassland classifications, using divergent methods. These classifications simplify prediction of grassland characteristics, which depend on the viewpoint and method of study.

Naturalists have used phytosociology since the early 20th century to classify vegetation communities and assess habitat conservation. The development of phytosociological

classification required botanical relevés of all vascular species and a coefficient of abundance-dominance for each species of each relevé (Braun-Blanquet, 1964). Phytosociology is the mainstream method for classifying vegetation communities as it can be applied to all ecosystems worldwide (e.g. Cheng et al., 2013; Rodríguez-Rojo et al., 2017, 2001; Setubal and Boldrini, 2012), vegetation classes are arranged into a hierarchical system, and their names follow scientific rules (Dengler et al., 2008). Once developed, the use of phytosociological classifications requires only a complete botanical relevé and less than an hour in each field. Phytosociology can also be used to predict agronomic characteristics, such as forage quality, and environmental characteristics by using indicator species (Petrovic et al., 2013); however, coefficients of abundance-dominance correlate only weakly with each species' percentage of total grassland biomass (i.e. relative biomass) , which can skew assessment of agronomic characteristics (Daget and Poissonet, 1971; Pittarello et al., 2018). Naturalists use phytosociology frequently worldwide; in the European Union, it is used to assess habitat conservation and define priority habitats to protect faunal and floral biodiversity.

Agronomists have developed agronomic classifications since the 1950s to quickly assess forage yield and quality, as well as impacts of practices on forage production and the environment (Michaud et al., 2013). Complete knowledge of botanical diversity is needed to develop a classification because effects of each plant species on animal production depend on its prevalence in an animal's diet (Diquélou et al., 2003), but classification approaches may vary. Agronomic classifications provide accurate information about agronomic performances of grasslands but are closely tied to the areas for which they were developed. Once developed, agronomic classifications can often be used without botanical knowledge, but they do require knowledge about agronomic practices, which needs to be collected when the classifications are developed. Doing so requires time, but can begin a discussion between farmers and agricultural advisors. Moreover, agronomic classifications can be used to predict ecological characteristics such as species richness and pollinator value (Hulin et al., 2011; Launay et al., 2011), but not all classifications have been developed for this purpose. Several agronomic classifications have been developed, especially in western Europe, and they are used by a wide range of decision makers, including agricultural advisors and farmers (Michaud et al., 2013).

More recently, during the 1990s, ecologists attempted to explain the functioning of grassland ecosystems using functional traits of plants (e.g. Lavorel and Garnier, 2002; Mouillot et al., 2013; Violle et al., 2007). A functional trait is "any morphological, physiological or phenological feature measurable at the individual level, … without reference to the environment or any other level of organization" (Violle et al., 2007). Agronomists applied this knowledge to permanent grasslands to develop functional classifications, which are used to predict grassland agronomic characteristics such as forage quality, earliness and management flexibility. Dominant grass (Cruz et al., 2010; Durante et al., 2012) and forb species have been classified by their functional traits, which are then used to classify grasslands. Functional ecology has brought a fresh perspective to ecology and agronomy, improved prediction of ecosystem goods and services, such as fodder production or carbon and nitrogen cycling (Carol Adair et al., 2018; Lavorel, 2013), and been particularly useful for characterising community response to environmental change (Lavorel and Garnier, 2002; Nock et al., 2016). Unlike agronomic classifications, functional classifications are not restricted to the areas for which they were developed (Cruz et al., 2010) and, once developed, do not require great botanical knowledge: the relative biomass of the grass and forb species classified is sufficient to classify the grassland and predict its agronomic characteristics. Developing functional classifications, however, requires knowledge about functional traits of plant species. These

classifications are already used in France to help farmers manage grasslands (Carrère et al., 2012).

The first objective of our study was to compare how phytosociological, agronomic and functional classifications assess grassland characteristics, as they use different methods and have different objectives. Phytosociological classification's main aim is to describe botanical associations, while agronomic classification focuses on predicting forage yield and quality. In comparison, functional classification predicts mechanisms (e.g. strategy for acquiring nutrients, development of plant structure) that express themselves when exposed to environmental variation. We hypothesised that each classification could predict certain characteristics well: phytosociological for ecological characteristics, agronomic for agronomic characteristics and functional for agronomic and environmental characteristics.

Classifications are used to predict grassland ecosystem goods and services, but usually only one classification approach is used to do so. However, differences in classification objectives lead to divergent methods for constructing classifications, which can cause classifications' predictions of grassland characteristics to differ despite having similar prediction potentials. From this perspective, the second objective of this study was to investigate prediction capacities of combined grassland classifications. To our knowledge, few studies have combined classification approaches. Carrère et al. (2012) combined phytosociological class, agronomic management and functional class to study potential evolution from one grassland class to another (e.g. due to modifying fertilisation or earliness of first use). Macedo et al. (2010) compared the species prediction abilities of three classifications of dune plants: phytosociological, dominant-strategy (Grime's CSR theory) and functional. They found that these classifications predicted plant species similarly but differed in their predictions of plant response to disturbance. However, Macedo et al. (2010) predicted ecological characteristics of dune communities only, and neither of these two studies assessed the increase in prediction accuracy provided by combinations of classifications. We hypothesised that although each classification has strengths and weaknesses, combined classifications would create a new classification that was more polyvalent and accurate at predicting grassland characteristics.

Using a sample of 250 permanent grasslands, we determined a phytosociological, agronomic and functional class for each. We analysed the prediction accuracy of each of the three classifications and explored whether combining two or all three of them improved prediction of each of 16 ecological, agronomic and environmental characteristics. Finally, we determined whether one classification alone or a combination of classifications could predict all 16 of the characteristics well.

2 Materials and methods

2.1 Site

The dataset consisted of 250 grasslands in the Vosges Mountains (north-eastern France, 7000+ km²) (Fig. 1). Their elevations vary greatly (170-1424 m a.s.l.), as does their geology: from limestone and sandstone in the north to plutonic volcanic rock in the south. The climate is under oceanic and semi-continental influences, and can be polar at mountain summits. According to climate normals (1981-2010), mean monthly temperatures vary from -4 to +12°C, and mean annual precipitation varies greatly (700-2300 mm) under complex latitudinal, longitudinal and elevational gradients (Ferrez et al., 2017). Finally, the Vosges Mountains cover a large gradient of agricultural practices: 26 % of the grasslands were exclusively mown, 38% were exclusively grazed, and nitrogen fertilisation ranged from 0-277

kg nitrogen/ha (69% organic (manure applied or directly deposited during grazing) and 31% synthetic, by mass).

2.2 Attribution of grassland classes

Three studies were performed from 2001-2013 (Bayeur et al., 2013; Collectif, 2006; Launay et al., 2011) of 250 permanent grasslands on commercial farms (Fig. 1). They focused on the main homogeneous vegetation community of each grassland in areas 1000-10,000 m² in size to avoid effects of paddock size on botanical diversity. One botanical relevé per grassland was performed in the spring (peak biomass production), identifying all vascular botanical species and their relative biomass (%) in 25 circles of 0.2 m² randomly placed in the homogeneous vegetation community. Finally, homogeneous vegetation community were prospected to search for species too rare to be found in the 25 samples.

353 species were observed in 250 grassland homogeneous vegetation communities. The mean (±SD) number of species per community was 37.6 (±8.7) [min-max = 16-65]. Thirty species formed 80% of the total biomass, with a dominance of red fescue *Festuca rubra* L. (14.9%), Yorkshire fog *Holcus lanatus* L. (9.1%), perennial ryegrass *Lolium perenne* L. (7.4%) and sweet vernal grass *Anthoxanthum odoratum* L. (5.6%). 11 threatened or endangered species were identified (seven vulnerable, two endangered and two critically endangered) according to the IUCN Red List, distributed in 30 grasslands. We used this dataset to attribute an agronomic, functional and phytosociological class to each of the 250 grasslands.

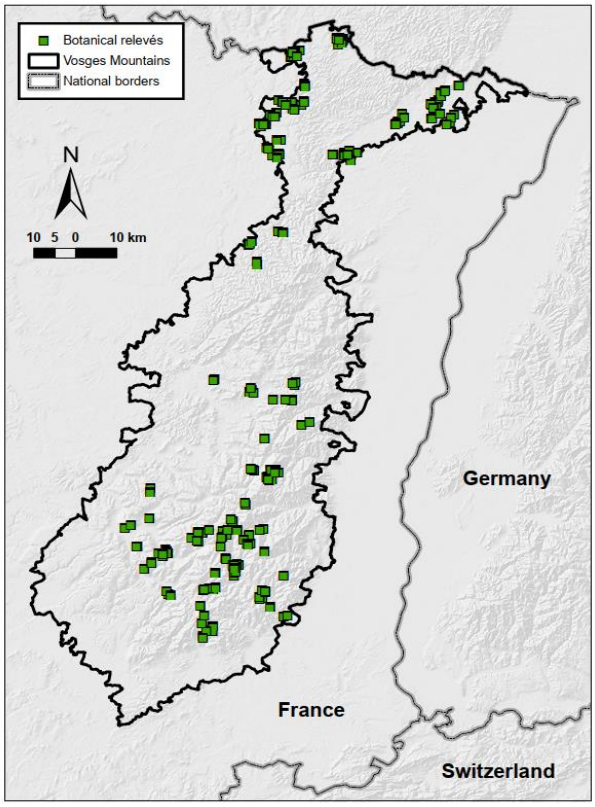

Figure 1. Location of the 250 botanical relevés performed in the Vosges Mountains, France, from 2001-2013 (Bayeur et al., 2013; Collectif, 2006; Launay et al., 2011). Coordinate system: RGF93-Lambert93

2.2.1 Agronomic class attribution

Previous studies identified 25 agronomic classes for homogenous grassland based on species presence and relative biomass (Bayeur et al., 2013; Collectif, 2006). To this end, they performed multivariate analyses of grassland composition: Correspondence Analysis (CA) and Hierarchical Cluster Analysis (HCA) of species presence and Principal Component Analysis (PCA) and HCA of relative biomass. Thus, by combining CA and PCA, they attributed one agronomic class to each grassland based on the presence and relative biomass of its botanical species (Table S1). The number of grasslands per agronomic class varied from 4-24 (Table 1).

This classification is called "agronomic" because its main aim is not to predict botanical associations, but to use these associations to predict forage yield and quality.

2.2.2 Functional class attribution

Cruz et al. (2010) attributed one class (A, B, b, C and D) to 38 of the most common French grasses (Poaceae), based on a combination of functional traits for leaves (dry matter content, specific leaf area, longevity, resistance to breakage) and plants (flowering date, maximum height) (Table S2). Then, Cruz et al. (2010) attributed functional classes to grasslands according to the percentage of each grass class in them.

We adapted their method of functional class attribution to reduce the number of grassland classes containing only one grassland. If one grass class represented more than 60% of grassland grasses, the grassland was defined as that class (e.g. 76% of grasses of class A, 3% of B and 21% of C yielded grassland class A), as proposed by Cruz et al. (2010). Otherwise, grassland was defined by the two main grass classes, in decreasing order (e.g. 28% of A, 30% of B, 10% of b and 32% of C yielded grassland class CB).

We then attributed one functional class to each permanent grassland based on the Cruz et al. (2010) grass classifications and the relative biomass of these grasses in each grassland. Thus, we attributed 20 functional classes, with 1-41 grasslands per class (Table 1). The mean (±SD) percentage of Poaceae in relevés was 64.8 ± 13.5% [min-max = 24.0-96.7%], while that of other families was 35.2 ± 13.5% [3.3-76.0%].

2.2.3 Phytosociological class attribution

Ferrez et al. (2017) developed a phytosociological classification for the entire Vosges Mountain range using 1628 relevés performed from 1993-2015 following the Braun-Blanquet method. They identified 35 phytosociological classes and selected the 22 of them that had the highest appearance rates and most important agronomic and ecological roles in the Vosges Mountains (Table S3). These 22 classes are based on 550 grassland relevés on commercial farms.

Normally, phytosociological classes are attributed directly in the field. For this study, however, we had to attribute phytosociological classes to the 250 grasslands *a posteriori*, from a dataset of existing botanical relevés. Therefore, we developed a new key to determine phytosociological classes. We used a statistical regression tree to design the new key, using the complete set of 550 relevés (Ferrez et al. 2017) and the mvpart package of R software v. 3.4.2 (R Core Team, 2019; Therneau and Atkinson, 2014). The key, based on 48 botanical genera, determines phytosociological classes easily. We verified the key's percentage of good classification for the dataset (550 grasslands) using a confusion matrix. According to the confusion matrix, the key had an agreement of 81%.

Using this key and the presence of botanical genus that we observed in each grassland during the field sampling from 2001-2013, we attributed a phytosociological class to each of the 250 studied grasslands. All of the following analyses were performed for these 250 grasslands.

Thus, we attributed 17 phytosociological classes to the 250 grasslands, with 3-61 grasslands per class (Table 1). As 22 classes could have been attributed at most, five classes were not observed in the set of grasslands.

Table 1. Number of grasslands (n = 250) attributed to 17 phytosociological classes, 25 agronomic classes and 20 functional classes when attributing one phytosociological, one agronomic and one functional class to each grassland (Table S1, S2 and S3).

Phytosociological classes		Agronomic classes				Functional classes	
Phy_12	61	BV_02	24	VN_09	14	C	41
Phy_05	25	BV_01	17	VN_07	13	A	40
Phy_01	24	BV_10	13	VN_12	11	AC	38
Phy_02	21	BV_06	12	VN_13	11	CA	31
Phy_11	20	BV_07	11	VN_05	9	AB	26
Phy_20	20	BV_08	11	VN_08	9	Ab	15
Phy_07	14	BV_03	10	VN_14	9	B	10
Phy_09	12	BV_04	10	VN_01	8	BA	8
Phy_25	9	BV_09	10	VN_02	8	Cb	8
Phy_04	8	BV_11	6	VN_06	8	CB	6
Phy_06	8	BV_05	5	VN_03	6	CD	6
Phy_08	8			VN_11	6	BC	5
Phy_16	6			VN_10	5	Bb	4
Phy_18	5			VN_04	4	bB	3
Phy_29	3					DC	3
Phy_30	3					bC	2
Phy_31	3					AE	1
						b	1
						bA	1
						E	1

2.3 Grassland characteristics

We chose to analyse ecological, agronomic and environmental characteristics of grasslands. Some of them were ecosystem services, which are benefits that people obtain from ecosystems (Millennium Ecosystem Assessment, 2005); however, this definition is still debated, and goods can be separated from services (Fisher et al., 2009). In addition, goods and services can be delivered by both the ecosystem and human practices; for example, grassland yield can be increased by applying synthetic fertilisers. Because we assessed a variety of goods and services delivered by the ecosystem and by human practices, we referred to them collectively as "grassland characteristics".

We selected nine ecological characteristics to assess taxonomic diversity (species richness, family richness, Shannon heterogeneity index, Simpson diversity index), functional diversity (life form abundance, pollinator value, richness and weighted mean of the Ellenberg root system depth index) and patrimonial functions (oligotrophic species richness, which can be used as a proxy for species of high ecological value, threaten by the homogenization and intensification of agricultural management). We selected three agronomic characteristics to assess actual forage quantity (yield), potential forage quality and quantity (pastoral value) and phenology (fodder earliness). Finally, we selected four environmental characteristics to assess the sensitivity of classification to natural and human factors (Ellenberg humidity and fertility indices, elevation and management). We used a variety of methods (e.g. calculation, farmer interviews) to determine the 16 characteristics (Table 2, S4 and S5).

The botanical relevés of 250 grasslands and interviews of 52 farmers were performed in previous studies, which were used to develop the agronomic classification (Bayeur et al., 2013; Collectif, 2006; Launay et al., 2011). Botanical relevés allowed the collection of species composition and relative biomass, which we entered into the e-FLORA-sys program (Plantureux and Amiaud, 2010, 2009). This program calculated information at the vegetation community scale: all ecological characteristics, as well as pastoral values and life form diversity came from direct observation and calculation by e-FLORA-sys. Using a questionnaire to avoid bias, farmers were interviewed to obtain information about yield and grassland management. Knowledge from the interviews were extracted to deduce grassland management ("mown", "grazed" or a "mixture" of both) and estimate yield from the number and mass of bales and from livestock stocking rates. On 14 grasslands, vegetation was sampled and dried to measured yields without interviews. Finally, grassland elevation was collected using BD ALTI dataset and QGIS software (IGN, 2016; QGIS Development Team, 2019).

Table 2. Methods for determining the 16 characteristics studied for permanent grasslands, in ecological, agronomic and environmental categories.

Characteristic		Determination method
Ecological	Species richness	Number of botanical species observed in the grassland
	Oligotrophic species richness	Number of botanical species observed in the grassland with an Ellenberg nitrogen index of 1-3
	Family richness	Number of botanical families observed in the grassland
	Shannon heterogeneity index	$-\Sigma(Yk \times \log_2 Yk)$, where Yk is the relative biomass of species k ($0<Yk\leq1$)
	Simpson diversity index	$1 - (\Sigma\ Yk^2)$, where Yk is the relative biomass of species k ($0<Yk\leq1$)
	Pollinator value	Relative biomass (% of total biomass) of entomophilous botanical species observed in the grassland
	Ellenberg root system depth index richness	Number of different Ellenberg root system depth indices observed in the grassland
	Ellenberg root system depth index weighted mean	$\Sigma(Yk \times$ individual root index), where Yk is the relative biomass of species k ($0<Yk\leq1$)
	Life form abundance	Relative biomass (% of total biomass) of each life form: grasses (Cyperaceae, Juncaceae, Liliaceae , Poaceae), legumes (Fabaceae) and forbs
Agronomic	Yield	Estimated from the number of bales and livestock stocking rate, or measured in the field
	Pastoral value	$\Sigma(Yk \times$ individual pastoral value), where Yk is the relative biomass of species k ($0<Yk\leq100$). For each species, pastoral value is estimated by expert opinion from potential yield, nutritive value, appetence and digestibility (Daget and Poissonet, 1971)
	Fodder earliness	Relative biomass (% of total biomass) of early, middle and late species, according to Cruz et al. (2010) and Theau et al. (2017)
Environmental	Ellenberg humidity index	$\Sigma(Yk \times$ individual humidity index), where Yk is the relative biomass of species k ($0<Yk\leq100$)
	Ellenberg fertility index	$\Sigma(Yk \times$ individual fertility index), where Yk is the relative biomass of species k ($0<Yk\leq100$)
	Elevation	Mean elevation of the grassland
	Management	“Mown”, “grazed”, or a “mixture” of both, obtained from farmer interviews

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2.4 Statistical analyses

We first identified the classification or combination of classifications that predicted each characteristic the best. We then assessed the quality of the best models to identify the most polyvalent classification or combination of classifications for all 16 characteristics. The specific method used depended on the grassland characteristic.

2.4.1 Modelling each characteristic with classifications

We used statistical model selection to calculate the probability that each classification alone (phytosociological (P), agronomic (A) or functional (F)), or a combination of classifications, yielded the best model, using R software. We modelled each characteristic as a function of each classification or combinations of classifications. To this end, we generated a model containing the main effects of all the classifications (A+P+F), and we then derived all possible submodels, including an intercept-only model (null model) (Burnham and Anderson, 2002; Grueber et al., 2011). We then repeated this methodology from a model containing the interactions of all the classifications (A×P×F). Thus, a set of 12 models could be created, based on classifications alone and combinations of classifications. The sets of models generated to predict each characteristic are presented in Table S6.

Combining agronomic and phytosociological classifications yielded 116 combinations (e.g. agronomic class BV_01 with phytosociological class Phy_05 for the same grassland). Similarly, we identified 136 combinations of agronomic and functional classifications, 93 combinations of phytosociological and functional classifications, and 202 combinations of all three classifications. The large number of combinations of classifications demonstrated that classifications differed in how they classified grasslands.

We modelled each continuous variable (species richness, oligotrophic species richness, family richness, Shannon heterogeneity and Simpson diversity indices, pollinator value, Ellenberg root system depth richness and root system depth index weighted mean, yield, pastoral value, Ellenberg humidity and fertility indices and elevation) using generalised linear models from the gamma family. We modelled each characteristics by 12 models.

We also fitted life form abundance and fodder earliness using generalised linear models. However, as we used only one model for life form (grass, legume and forb) and one model for earliness (early, middle and late), models were created from the binomial family. Here again, we modelled each characteristics by 12 models.

Grassland management was a categorical variable, so we created multinomial logit models using the mlogit package (Croissant, 2015). As logit models do not support interactions (Croissant, 2015), we fitted only eight models to grassland management.

2.4.2 Identification of the best model

After creating the models, we selected the best one for each characteristic. Except for grassland management models, the best model was that with the lowest second-order Akaike Information Criterion (AICc), calculated using the MuMIn package and R software (Barton, 2018). Grassland management models were ranked according to the Akaike Information Criterion (AIC) itself, calculated using the qpcR package and R software (Spiess, 2014), because AICc cannot be calculated for logit models (Barton, 2018).

During model selection, an Akaike weight (hereafter, “weight”) is attributed to each model tested. This weight is the probability that a given model is the best, and the sum of the weights of all models tested equals 1 (Symonds and Moussalli, 2011). For each analysis, we compared

the weight of each model to those of other models: the closer a model's weight is to 1, the better the model is. If only one model had a high weight (> 0.8), we assumed it was the best, but if several models had similar weight, we examined them more closely. We verified the quality of the model selection by ensuring that the null model had a weight close to zero (Symonds and Moussalli, 2011).

2.4.3 Identification of a reliable polyvalent classification

Best model do not mean good model: the best among poor quality models remain a poor quality model. Moreover, the best model for a given characteristic may not be the best model for multiple characteristics together. To solve these two issues, we calculated the quality of each best model. First, model quality informed about the accuracy of each characteristics model. Then we could compare the accuracy of models selected for several characteristics: if a model would be selected as best model for several characteristics and its accuracy would be sufficient, we could assume it is a polyvalent and reliable model.

AIC and AICc indicate model quality, but as they are relative to the dataset for each characteristic we could not use them to compare best models for multiple characteristics (Burnham and Anderson, 2002). We used each best model to predict all 16 characteristics and calculated a goodness of fit among the predictions using pseudo-R^2, because R^2 cannot be calculated for generalised linear models (Tjur, 2009).

For generalised linear models for the gamma family, we calculated Cox and Snell pseudo-R^2 (Cox and Snell, 1989), which is the easiest to use because it expresses R^2 in terms of log-likelihood (Tjur, 2009). Because the Cox and Snell pseudo-R^2 is not optimal for generalised linear models from the binomial family or for multinomial logit models (Cox and Snell, 1989), we calculated McFadden's pseudo-R^2 for these models, which is also based on the likelihood of the model (Hoetker, 2007). We used the DescTools package and R software to calculate pseudo-R^2 (Signorell, 2017). Finally, we calculated generalised variance-inflation factors to check for collinearity among models, using the car package (Fox and Sanford, 2011). We assumed that models with pseudo-$R^2 > 0.5$ had a satisfactory goodness of fit.

3 Results

3.1 Identification of the best classification

The model with the highest weight for 15 of the 16 grassland characteristics contained one or more classifications, as root system depth richness was predicted best by the null model (Fig. 2). Among these 15 models, four of them had a weak weight <0.8 and required a closer look to identified best models: Shannon heterogeneity index (0.66), pollinator value (0.52), Ellenberg root system index weighted mean (0.73) and Ellenberg fertility index (0.59).

One classification alone was sufficient to predict four characteristics the best. Three characteristics were predicted best by agronomic classification alone (A): yield (agronomic), grassland management (environmental) and elevation (environmental). One characteristic was predicted best by phytosociological classification alone (P): species richness (ecological).

For two characteristics, the model with the highest weight contained only one classification, but the weight was not high enough to select it as the best model. For Shannon heterogeneity index, phytosociological classification (P) alone had the highest weight (0.66), but it did not differ enough from the second highest weight (0.25), which was for the main effects of phytosociological and functional classifications (P+F). Similarly, for pollinator value, weights

of agronomic classification (A) and the null model (0.52 and 0.35, respectively) were too similar to identify one best model.

The main effects of two or three classifications predicted six characteristics the best: agronomic and phytosociological (A+P) for family richness; agronomic and functional (A+F) for Ellenberg humidity index; phytosociological and functional (P+F) for Simpson heterogeneity index and pastoral value; and all three classifications (A+P+F) for fodder earliness. Ellenberg root system index weighted mean highest weight was associated to the P+F model, but was <0.8. However, the second highest weight was different enough to assume Ellenberg root system index weighted mean was best model by the main effects of phytosociological and functional classifications.

On the other hand, weights of the A+P+F and A+P models for the Ellenberg fertility index were too similar (0.59 and 0.41, respectively), we could not identify which one was best. Finally, two best models contained an interaction: that between agronomic and phytosociological classifications (A×P) for life form abundance, and between phytosociological and functional classifications (P×F) for oligotrophic species richness.

The highest weights equalled 1.0 for seven characteristics, 0.7-1.0 for six characteristics, and less than 0.7 for the Shannon heterogeneity index, pollinator value and Ellenberg fertility index. Null model weights equalled zero, except for those for pollinator value (0.35) and root system depth richness (1.0).

3.2 Identification of a reliable and polyvalent classification

The goodness of fit (pseudo-R^2) varied greatly among the best models for characteristics (0.20-0.88) (Fig. 2). The goodness of fit of the model for the Ellenberg root system index weighted mean equalled zero, due to the selection of the null model. Models for agronomic and environmental characteristics had high weights and/or quality. In contrast, most models for ecological characteristics had low quality, except for life form abundance, oligotrophic species richness and, to a lesser extent, family richness (pseudo-R^2 = 0.87, 0.83 and 0.54, respectively). We identified ten grassland characteristics whose models had goodness of fit > 0.5 (Fig. 3): oligotrophic species richness, family richness and life form abundance (ecological); yield, pastoral value and fodder earliness (agronomic); and Ellenberg indices for fertility and humidity, elevation and management (environmental). Unlike these ten grassland characteristics, the other six, all ecological, had best models of low quality despite having high weights: species richness, Shannon heterogeneity index, Simpson diversity index, pollinator value and richness and weighted mean of Ellenberg root system depth

We could not identify one polyvalent and reliable classification or combination of classifications that could predict ecological, agronomic and environmental characteristics well. Only agronomic classification could predict characteristics the best when alone, with high quality models. Moreover, most of the characteristics predicted well were predicted totally or partially by agronomic classification. The combination of phytosociological and functional classifications predicted oligotrophic species richness and pastoral value well.

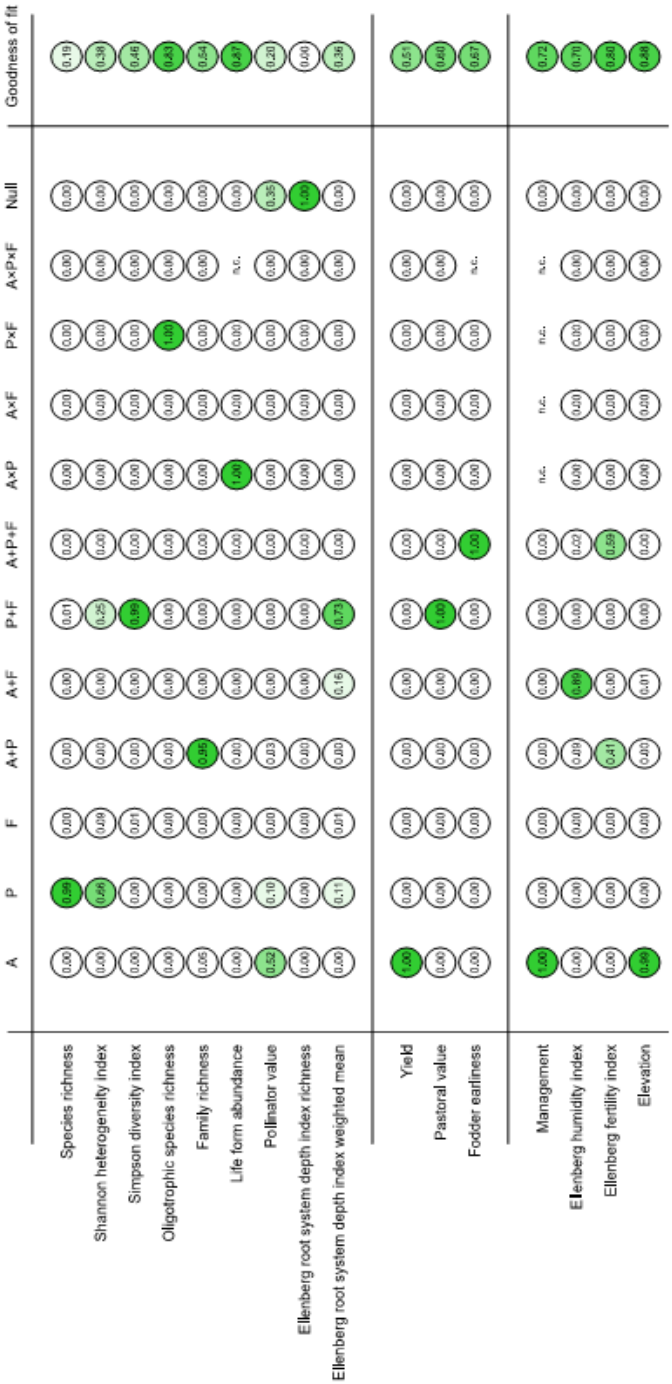

Figure 2. Akaike weights and goodness of fit (pseudo-R^2) of the 16 grassland characteristics modelled using agronomic (A), phytosociological (P) or functional (F) classification, the main effects of two or all three of them (A+P, A+F, P+F and A+P+F), their interactions (A×P, A×F, P×F and A×P×F) and a null model (Null). The term "n.c." ("not considered") indicates characteristics that could not be modelled with interactions. The goodness of fit shown is that of the model with the highest weight for each grassland characteristic.

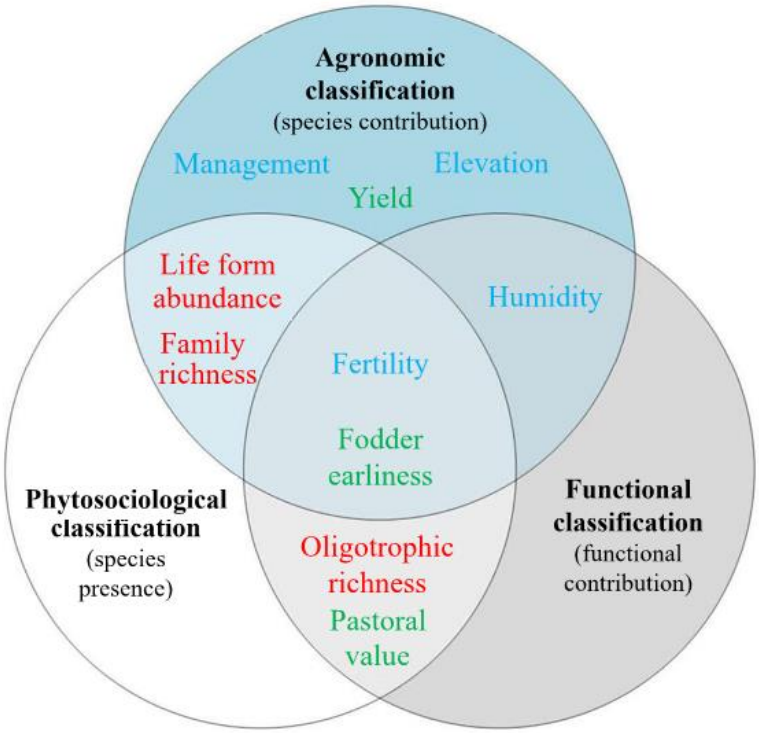

Figure 3. Representation of which phytosociological, agronomic and functional classifications (or combinations of them) were needed to predict ten grassland characteristics well (goodness of fit > 0.5). Red, green and blue text identify ecological, agronomic and environmental characteristics, respectively.

4 Discussion

4.1 Prediction of grassland characteristics

4.1.1 Quality of prediction models

Four of the six characteristics whose models had goodness of fit < 0.5 involved species or trait richness and equitability. This poor prediction of ecological characteristics is not surprising for agronomic and functional classifications, which were not designed to predict them and rely mainly on relative biomass rather than presence of species. The best models for each of these characteristics are built in part on phytosociological classification, except those for pollinator value and Ellenberg root system index weighted mean. However, the poor quality of these ecological characteristics highlights the lack of a relationship between ecological characteristics and phytosociological classification, which is more surprising. While grasslands in the same phytosociological class have species in common (a "characteristic combination"), they also have some different species among them, which gives them different values of species richness and may help explain our result. Bias in relevés could also be a reason: Chytrý (2001) showed that botanists increase the area sampled in species-poor grasslands to increase the number of species, which could bias attribution of class and calculation of richness.

Despite its common use and importance for estimating total biodiversity, species richness is not a key characteristic to predict because of its high variability in similar grasslands (Brunbjerg et al., 2018). These limits to biodiversity measurements have led researchers and decision-makers to use diversity indices such as the Shannon heterogeneity index and

Simpson diversity index (Bello et al., 2010; Mauchamp et al., 2014). In our study, we could not identify models that predicted diversity indices well, but ecological indices were predicted best by phytosociological classification alone or a combination of phytosociological and functional classifications. These indices provide different types of information: the Shannon heterogeneity index describes species equitability, while the Simpson diversity index describes both species equitability and richness. One way to predict grassland plant diversity well could be to use disturbance intensity: Vujnovic et al. (2002) showed that intermediate disturbance by grazing, trampling or soil management maximised grassland biodiversity, while Rodríguez-Rojo et al. (2017) observed that management intensity had more influence on grassland biodiversity than management practices. However, biodiversity measurement, through species richness or ecological indices, is not necessary a useful indicator. Indeed, these measurements do not take into account vegetation characteristics as proportion of rare species, which is not correlated to total richness (Pykälä et al., 2005). Assessment of biodiversity should be implemented with proxy for species of high ecological value like oligotrophic species richness (Michaud et al., 2012; Muller, 2002). In the present study, oligotrophic species richness was predicted best by the combination of phytosociological and functional classifications.

Among ecological characteristics, only pollinator value and the weighted mean of Ellenberg root system depth needed species relative biomass in their calculations. However, they are based on traits (pollinator attractiveness traits and root system depth, respectively) not included in the functional classification studied nor in other classifications. Agronomic classification has been used to estimate pollinator value (Bayeur et al., 2013; Hulin et al., 2011; Launay et al., 2011). Our study confirms that agronomic classification predicts pollinator value the best, but its low model quality (weight = 0.52, pseudo-R^2 = 0.20) raises questions about the reliability of the prediction. Beyond our study, phytosociological classification may help predict pollinator species or traits, which are particularly related to flower diversity (Hegland and Totland, 2005; Warzecha et al., 2017). However, entomophilous botanical species relative biomass assesses a potential pollinator value at grassland scale. To assess a real pollinator service, flowering time and cutting/grazing dates should be studied because they express the real abundance of flowers (Kleijn et al., 2001). The landscape also influences pollinator diversity and abundance strongly, but it is not included in grassland classifications (Sutter et al., 2017). Finally, our modelling of root system depth is similar to the study of Oram et al. (2018), which found that mean root system depth was related to other characteristics but root system depth richness was not.

4.1.2 Grassland characteristics predicted by one classification alone

Three grassland characteristics – elevation, management and yield – were predicted best by agronomic classification alone, which was the only classification that could predict grassland characteristics well by itself (Fig. 3). Management and elevation predict species composition well (Rodríguez-Rojo et al., 2017; van Oijen et al., 2018), and agronomic classification predicted management and elevation well with high weights and model qualities. We can assume that botanical associations developed from taxonomic relative biomass are good indicators of elevation and might be indicators of climate more generally.

Prediction of yield is crucial, especially for farmers. As agronomic classifications are developed mainly to predict agronomic characteristics, we expected a strong relationship between yield and agronomic classification. Functional classifications are also developed to predict grassland yields, and this ability was confirmed by Lavorel and Garnier (2002), who identified strong relationships between nutrient-response traits and traits determining yields. Plasticity in trait expression (at the species scale) and trait co-occurrence (at the community

scale) of grasses and forbs need to be better understood to improve predictions of functional classification (Roscher et al., 2018). Yield can be estimated easily using Ellenberg fertility index (Hill and Carey, 1997) or by more complex models based on functional traits, life form abundance (Michaud et al., 2015) and phytosociological classes (Magiera et al., 2017). Finally, field measurement also estimates grassland yield well but requires more time and equipment than using grassland classifications or Ellenberg indices (Ni, 2004).

4.1.3 Combining classifications: a solution?

To our knowledge, our study is the first to compare three classification approaches using the same relevés. Carrère et al. (2012) created tool based on phytosociological, agronomic and functional classifications but did not compare the quality of predictions provided by each classification to those of the combination of two or three classifications. Macedo et al. (2010) compared the prediction abilities of three classifications but focused only on predicting ecological characteristics of dune communities.

In our study, seven of the characteristics studied were predicted better by combinations of classifications than by one classification alone (Fig. 3): oligotrophic species richness, family richness and life form abundance (ecological), pastoral value and fodder earliness (agronomic) and Ellenberg humidity and fertility indices (environmental). Notably, among the goodness of fit >0.8, three out of four models required combination of classifications: life form abundance (0.87), oligotrophic species richness (0.83) and Ellenberg fertility index (0.8). Moreover, despite its weak prediction capacities when used alone, phytosociological classification is part of these three best models.

Both fertility and humidity indices were predicted well (high weight and goodness of fit) by combining classifications. Humidity and fertility indices have been linked to elevation (de Almeida Campos Cordeiro and Neri, 2019; Pittarello et al., 2018; Sevruk, 1997) but also to taxonomic (Critchley et al., 2002; Melts et al., 2018; Wang et al., 2007) and functional (Čop et al., 2009; Schellberg, 1999; Suding et al., 2005) diversity. We also used the fertility index to calculate oligotrophic species richness. However, fertility needed all three classifications to be predicted well, while oligotrophic species richness needed only phytosociological and functional classifications and was predicted better. This difference could have been due to the method used: the fertility index is based on relative biomass, unlike oligotrophic species richness. Ellenberg fertility index is influenced by fertilizer application, but is also dependant of soil properties like the cation exchange capacity. Thus, the prediction of Ellenberg fertility index and oligotrophic species richness can bring information about presence of species of high ecological value, but cannot be used to assess the impact of fertilization at scales larger than grassland community.

Life form abundance, as well as root system depth, was not included in previous classifications. The latter was not predicted well, but the life form abundance was predicted well by an interaction between classifications (A×P). This result is particularly interesting because it shows that grassland classifications can predict characteristics beyond those for which they were developed. Moreover, family richness was predicted best by a similar combination of classifications: the main effects of agronomic and phytosociological classifications (A+P). These characteristics are related by the method of calculation. Indeed, life forms are based on botanical families: legumes belong to Fabaceae, while grasses belong to Cyperaceae, Juncaceae, Liliaceae and Poaceae. This result could highlight a correlation between richness and relative biomass of families. Grassland management influences life form diversity strongly: mowing increases grass and forb relative biomass, while grazing selects rosettes and creeping plants (Gaujour et al., 2012; Lanta et al., 2009). However,

intensification also selects rosettes and creeping plants (Gaujour et al., 2012), and livestock type also has a strong influence on life form diversity (Tóth et al., 2018). These previous studies show that knowledge about grassland management could improve prediction of life form abundance; however, Craine et al. (2001) identified correlations between leaf traits and life form but no correlation between intensification and life form. The prediction of life form abundance can be useful for agronomists and naturalists. Indeed, grassland with highest life form diversity produce higher yields (Bullock et al., 2006), and allow heavier livestock live weight than grassland with poor life form diversity (Grace et al., 2019). In the present study, the goodness of fit of life form abundance (0.87) was higher than goodness of fit of yield (0.51) and fodder quality (0.60). Finally, life form abundance also determines the resistance of botanical species to drought: life form of weak abundance have more probabilities to disappear (Tilman and Haddi, 1992). Thus, life form abundance could be an important characteristic for naturalist who want to assess the risk of extinction of grassland botanical species.

It was particularly surprising that phytosociological and functional classifications combined (P+F) predicted pastoral value the best, because i) yield, part of the pastoral value equation, is predicted well by agronomic classification, and ii) calculating the pastoral value requires the pastoral value and relative biomass of each species, which is provided by agronomic classification (Daget and Poissonet, 1971). Functional traits (Tasset et al., 2019) and phytosociology (Petrovic et al., 2013) can be used to predict forage quality, but our result shows that combining them improves predictions. Phytosociology alone may not be sufficient to predict pastoral value due to the inclusion of different facies in the same phytosociological class (Bagella and Roggero, 2004). Prediction of pastoral value could be improved by using Ellenberg fertility index and environmental indicators such as elevation and slope (Bagella and Roggero, 2004; Pittarello et al., 2018).

Forage earliness is key information in grassland management, because peak forage quality is related to plant phenology (Pontes et al., 2007). Moreover, coupled with cutting or grazing dates, earliness could also be used to assess pollination service (Kleijn et al., 2001). Climate is the main factor that influences flowering time: temperature (Kudernatsch et al., 2008) and, to a lesser extent, precipitation (Hovenden et al., 2008) create annual variability. We used degree days to be free from annual temperature variability. Generally, alpine vegetation needs fewer heat units to initiate flowering (Heide, 1994), which could create a fodder earliness gradient according to elevation. Management, expressed indirectly through botanical composition, creates differences in earliness of French grasslands, but differences are also perceptible among species from the same community (Ansquer et al., 2009). We conclude that the three classifications are essential to predict fodder earliness: while the functional classification is based in part on grass earliness, phytosociological and agronomic classifications could provide information about other species.

4.2 Limits of the study and perspectives

It may be possible to extrapolate results of this study. From the viewpoint of environmental conditions, our study focused on 250 permanent grasslands of the French Vosges Mountains but covered wide gradients of climates, elevations, soils and agricultural practices. From the viewpoint of vegetation, we found 17 phytosociological classes out of the 35 identified by botanists in the Vosges Mountains (Ferrez et al., 2017). However, these 17 classes are the most representative of commercial farms according to expert opinion and can be found in many other lowlands and low-elevation mountains in western Europe. Finally, the functional classification studied can also be used in a wide range of grasslands, as it is representative of western-European grassland Poaceae (Cruz et al., 2010).

All grassland classifications are based in part on arbitrary choices, either of the classification criteria (here, taxonomic richness, taxonomic relative biomass, or functional relative biomass) or the number of grassland classes. The method used to attribute functional classes provided quick and easy classification, but it can also be restrictive and attribute different functional classes to similar grasslands. This method also creates several functional classes containing few grasslands: seven classes contained less than five grasslands. Moreover, the functional classification focused only on Poaceae, even though other families represent a relatively large percentage of each grassland (mean ± SD = 35 ± 14%), which could lead to lower accuracy in measuring response traits if Poaceae respond differently to disturbances than other plant families. A new functional classification based not only on Poaceae but also on dicotyledonous species may improve prediction abilities of functional classification. Finally, including new classification approaches should also improve knowledge about predicting grassland characteristics. Phytosociology diverges into two approaches: Braun-Blanquet and, more recently, numerical (Dengler et al. 2008). In the latter, relevés are grouped into classes using statistics, based on presence/absence (as in the Braun-Blanquet approach) or relative biomass (as in agronomic classifications). Classes are not phytosociological classes from the literature but are instead free from the subjective concept of the vegetation unit.

Of the 16 characteristics studied, five were calculated using Ellenberg indices, whose use may raise some questions. Indeed, some indices are estimated rather than measured, species response to the environment depends on location and plant stage, and the strength of correlations between indices and field measurements diverges among studies (Diekmann, 2003; Schaffers and Sýkora, 2000). Nevertheless, Ellenberg weighted mean indices are considered reliable (Diekmann, 2003).

In a more extensive study, we could have analysed the ability of grassland classifications to predict other characteristics. Classifications have been used to predict organoleptic characteristics of animal products (Diquélou et al., 2003) and soil carbon stocks (Hulin et al., 2011), but other services could be studied, such as maintenance of genetic diversity, regulation of water flows and landscape heritage (D'Ottavio et al., 2017). Moreover, a more complete dataset of grassland characteristics could improve statistical analyses: the lack of homogeneity of grasslands per class might induce statistical bias, and it is important to assess the quality of new models on an external dataset.

Our study raises questions about the use of phytosociological classification alone to identify habitats of interest in Europe. Indeed, we demonstrated that ecological characteristics remain difficult to predict and, above all, that phytosociological classification alone does not predict grassland characteristics well. However, identification of ecological characteristics could lead to conservation of key grasslands, while identification of agronomic characteristics could improve distribution of economic incentives for ecologically valuable grasslands. Characteristics can be predicted more accurately by combining classifications, as in this study, but also by using other methods. Indicator species or life traits such as life forms or flower colour are also easy to use but might be less accurate or more time consuming (Arnold et al., 2009; Ellenberg et al., 1992). Finally, models can consider soil and weather variability, but such models are often difficult for non-specialists to use and do not predict agronomic and ecological characteristics at the same time (van Oijen et al., 2018).

5 Conclusion

Our study focused on the ability of three classification approaches to predict 16 grassland characteristics. Our results show that agronomic classification has great potential to predict

three agronomic and environmental characteristics, which demonstrates that it meets the needs of farmers and agronomists well. Although phytosociological classification is designed to assess habitat conservation, it failed to predict the studied ecological characteristics well. Functional classification appears promising, but it was developed more recently and may suffer from knowledge gaps. As ecological characteristics remain especially difficult to predict, naturalists and policy makers should use tools other than phytosociological classification alone to predict them. Indicator species or life traits such as life forms or flower colour are also easy to use but might be more time consuming than a phytosociological relevé. To identify trade-offs between economics and ecology, it may be important to combine grassland classifications: our results show that combinations of phytosociological, agronomic and/or functional classification could accurately predict seven ecological, agronomic and environmental characteristics. Finally, models may improve prediction of characteristics: they can consider soil and weather variability but are often difficult for non-specialists to use and do not predict agronomic and ecological characteristics at the same time.

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