**The functional characterization of grass- and shrubland
ecosystems using hyperspectral remote sensing: trends, accuracy
and moderating variables**

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Abstract

Hyperspectral remote sensing is increasingly being recognized as a powerful tool to map ecosystem properties and functions through time and space. However, general information on the accuracy of this technology to assess the vegetation's biophysical and -chemical trait composition, and on the variables which are mediating this accuracy, is often lacking so far. Here, we addressed this knowledge gap for grass- and shrubland ecosystems and applied novel three-level meta-analytical regression equations to 77 studies that validated hyperspectral remote sensing data with field observations. Our results showed that the accuracy of hyperspectral sensors is generally high, but strongly depends on the trait being studied (leaf area index: $R^2 = 0.79$ and $nRMSE = 0.19$, chlorophyll: $R^2 = 0.77$ and $nRMSE = 0.21$, carotenoids: $R^2 = 0.80$ and $nRMSE = 0.29$, phosphorus: $R^2 = 0.76$ and $nRMSE = 0.14$, nitrogen: $R^2 = 0.74$ and $nRMSE = 0.09$, water: $R^2 = 0.69$ and $nRMSE = 0.13$, and lignin content: $R^2 = 0.64$ and $nRMSE = 0.26$). Moreover, they indicated that the use of multivariate signal processing techniques could improve these estimation accuracies (adjusted $p < 0.06$ for LAI, chlorophyll and nitrogen). Finally, estimations from air- and spaceborne imaging spectrometers, allowing for functional mapping at broader spatial scales, were found to be as accurate as estimations from ground-based spectral measurements. Despite these promising findings, we revealed that leaf morphological properties (e.g. specific leaf area and leaf dry matter content) and biochemical traits which are not growth-related (e.g. lignin and cellulose) remain underexplored in grass- and shrublands. Moreover there was a strong publication bias towards R^2 for assessing model performance. Our findings foster and direct further methodological and technological developments for a more accurate and complete functional characterization of these ecosystems worldwide.

42 **Keywords**

43 Meta-analysis, grassland, shrub, hyperspectral remote sensing, imaging spectroscopy, plant
44 functional traits, LAI, nitrogen, phosphorus, chlorophyll, carotenoids, lignin, water content

1. Introduction

The evaluation of management and climate impacts on the Earth's life support system requires an understanding of ecosystem dynamics. The concept of plant functional traits can highly contribute to such understanding (Díaz et al., 2004; Orwin et al., 2010; Shipley et al., 2006). It enables the assessment of plant communities response to environmental change and anthropogenic pressures on the one side (de Bello et al., 2006; Garnier et al., 2007), and the prediction of alterations in the functioning of ecosystems due to changing plant communities on the other side (Kurokawa et al., 2010; Lavorel and Garnier, 2002). Today, a wide range of morphological, physiological and phenological plant characteristics have already been successfully linked to ecosystem properties and processes such as biomass production, soil fertility and biogeochemical cycles (de Bello et al., 2010; Díaz et al., 2007; Lavorel and Garnier, 2002). Easily available and large scale information on the functional composition and diversity of plant communities is hence crucial for tracking the status of Earth's ecosystems (Chapin et al., 2000; Lamarque et al., 2014).

Although the traits of plant species can be manually measured (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013) and are widely available in various local (Kleyer et al., 2008; Paula et al., 2009) and global (Kattge et al., 2011) databases, these actually cover only about 2% of currently known vascular plant species (Jetz et al., 2016). Part of the explanation for this lack of data is that measuring functional traits in the field or laboratory is laborious and may even be unfeasible, especially in very diverse ecosystems or at very large geographical scales (Homolová et al., 2013). Even though techniques exist to fill taxonomical and functional data gaps (e.g. Schrodte et al., 2015; Shan et al., 2012; Taugourdeau et al., 2014) and to upscale available trait data to larger geographical scales (e.g. Swenson et al., 2012; van Bodegom et al., 2014), these approaches remain hampered by sample inhomogeneities and do not account for temporal variations. Remote sensing, allowing spatially continuous and frequent observations

across ecosystems, is an established technique to map structural and biochemical plant properties (Curran, 1989; Homolová et al., 2013; Ollinger, 2011; Ustin et al., 2009). More recently this potential has been acknowledged in biodiversity science, for example in the mapping of plant species diversity (Asner and Martin, 2016; Lausch et al., 2016; Zhao et al., 2016), plant strategies (Fassnacht et al., 2017; Feilhauer et al., 2016; Schweiger et al., 2017) and invasive plants (Niphadkar and Nagendra, 2016).

Although studies quantifying plant traits using hyperspectral sensors or imaging spectroscopy are numerous, they are to some extent biased towards forest and agro-ecosystems (Asner et al., 2015; Dorigo et al., 2007; Knyazikhin et al., 2013). Despite the extent and ecological value of grass- and shrubland ecosystems, their functional characterization using hyperspectral remote sensing is still somewhat underexplored. Covering up to 40% of the global land area (Latham et al., 2014; Suttie et al., 2005; White et al., 2000) they include among the most species-rich plant communities (Faber-Langendoen and Josse, 2010; Pinches et al., 2013; WallisDeVries et al., 2002), providing essential habitats for other species (Silva et al., 2008; Van Swaay, 2002). These ecosystems play an important role in the functioning of Earth's life system by regulating water quality (Rowe et al., 2006; Stevens et al., 2008), protecting soil from water and wind erosion (De Baets et al., 2006; Li et al., 2007) and sequestering carbon (Derner and Schuman, 2007; Minami et al., 1993).

Despite the exhaustively described potential of remote sensing for mapping and monitoring the status of vegetation in grasslands (Ali et al., 2016), rangelands (Svoray et al., 2013) and wetlands (Adam et al., 2010), we lack a general quantitative assessment of the reliability of remote sensing to quantify a range of ecosystem properties and functions, and of the variables affecting this reliability. This information is crucial for the further adoption of remote sensing techniques in biodiversity science, given the increasing availability and affordability of data generated by hyperspectral sensors. Here we filled this knowledge gap through a

comprehensive meta-analysis of trait estimation accuracies obtained with different hyperspectral sensors in grass- and shrublands worldwide. Data-driven meta-analyses combine results across studies, generally assigning more weight to more precise studies, and by doing so improve statistical power compared to individual studies (Borenstein et al., 2009; Curtis and Queenborough, 2012; Lipsey and Wilson, 2001).

Next to quantifying overall trait estimation accuracies, the meta-analytical approach is highly useful to reveal technical and methodological trends in the collection of relevant articles. First, as a result of the progress in sensor technology, a wide variety of handheld and airborne hyperspectral sensors are nowadays operational (Qi et al., 2011). Meanwhile, the increasing interest in large-scale ecosystem functioning and biodiversity (Pereira et al., 2013; Proença et al., 2016; Skidmore et al., 2015) is driving the development of hyperspectral space missions such as EnMAP (Segl et al., 2010; Stuffer et al., 2007), HypsIRI (Pellissier et al., 2015; Turpie et al., 2015) and PRISMA (Labate et al., 2009). The utility of these sensors for global diversity and global change studies will depend on whether satisfying accuracies can be obtained when capturing information at coarser resolution. Second, a large variety of signal processing techniques is available, with different technical strengths and weaknesses (Atzberger et al., 2015; Verrelst et al., 2015). Recently, emphasis has shifted from the use of vegetation indices towards multivariate modelling, where a larger part of the spectrum is used for trait quantification (Verrelst et al., 2015). Because statistical approaches often lack generalization potential and transferability to different images or conditions (Dorigo et al., 2007; Foody et al., 2003), radiative transfer models have been developed which, based on physical principles, disentangle the contribution of structural and biochemical characteristics, but also illumination geometry and soil background characteristics to the spectral signature. In herbaceous ecosystems, mainly the PROSAIL canopy reflectance model (Jacquemoud et al., 2009), combining the PROSPECT leaf optical properties model (Jacquemoud and Baret, 1990) and

the SAIL canopy bidirectional reflectance model (Verhoef, 1984), has been exhaustively applied and validated (e.g. Darvishzadeh et al., 2008a). The extent to which the computational complexity of enhanced methods is worth the effort in terms of trait estimation accuracy will influence researchers in making methodological choices.

In this study we sought to quantitatively synthesise previous research on the functional characterization of grass- and shrubland ecosystems using hyperspectral remote sensing. Our specific aims were to:

- (i) determine geographical distribution patterns of published studies and to identify research trends in the use of different sensor scales and signal processing techniques over time;
- (ii) determine the overall estimation accuracy and precision of several key grass- and shrubland traits;
- (iii) evaluate the potential of airborne and satellite missions for detecting functional traits in comparison with ground-based hyperspectral measurements; and to
- (iv) explore the capacities of different signal processing techniques for estimating functional traits.

2. Materials and methods

2.1 Literature search and criteria for inclusion

In order to assemble a representative sample of studies quantifying functional traits with hyperspectral data in grass- and shrubland ecosystems, two procedures were followed. First, we conducted an extensive database search of Thomas Reuters Web of Science using combinations of keywords looking for 1) hyperspectral studies in 2) grass- and shrubland ecosystems, investigating 3) plant functional traits (Table S1). We focused on a wide variety of quantitative

biochemical and structural traits which are easy to measure in the field/laboratory (Garnier et al., 2016), have a clear expression in the vegetation's spectral signature (Ollinger, 2011), and support multiple interdependent functional processes. These included light capture and growth biochemicals such as pigments, nitrogen and phosphorus, essential supporting compounds such as water and lignin, and morphological leaf and plant properties such as LAI, SLA and canopy height (Table S1). Although from a forage quality perspective for livestock industry several other characteristics such as crude protein and ash content, metabolizable energy, acid and neutral detergent fibre are interesting (Beeri et al., 2007; Pullanagari et al., 2012), we did not include these traits in our meta-analysis. The keywords were combined with Boolean AND's (between the three search strings) and Boolean OR's (within each search string). No restrictions were set on document type and time span. Our most recent search (April 10th, 2017) identified 483 publications. In addition to the systematic database search, we examined the reference sections of relevant literature reviews for additional publications.

From the retrieved list of studies, only these were retained that (i) focused on non-agricultural grass- and shrublands, (ii) reported R^2 and/or nRMSE (i.e. RMSE expressed as a percentage of the mean trait value) as measure of trait estimation precision and accuracy, and (iii) reported the number of samples used for model development and/or testing. The coefficient of determination and normalized root mean square error were selected over other goodness-of-fit statistics because they were most frequently reported in the identified studies, or derivable from the text and figures. Moreover, the non-dimensionality of both indicators allows for comparability and therefore enabled us to combine studies expressing traits in different units and scales. Lastly, because they indicate different aspects of a model's performance, the sole consideration of one indicator is strongly discouraged for assessing trait estimation accuracy (Richter et al., 2012).

2.2 Data extraction

A typical study reported multiple estimation results, associated with different spectral datasets varying across sampling site, measurement period and/or sensor type. For each such unique combination, the best model statistics (which we defined as the highest, respectively lowest, reported calibration, resampling and/or validation R^2 and nRMSE) were considered and coded for each of the variables presented in Table S2. If different signal processing techniques were investigated in a study, they were separately coded and included in the database. Each record/row of the trait database hence corresponded to the best estimation result obtained by a certain signal processing technique and based on a particular spectral dataset. This coding procedure was carried out for each trait considered in our meta-analysis.

We identified four variables which could possibly have a moderating impact on trait estimation accuracy:

- i. **Sensor scale:** Many hyperspectral sensors are in use for measuring vegetation characteristics, operating in space (satellites), air (planes, helicopters and UAV's) or at ground level (proximal sensing). While the first two sensor scales inherently are restricted to canopy measurements, ground based measurements encompass both canopy and leaf measurements. These four operating systems were adopted as sensor scale levels in our study. In the two ground based categories we included both field measurements and measurements executed under standard conditions in a laboratory. Because some authors resampled ground based spectral measurements to the spectral resolution of airborne and satellite sensors prior to trait quantification, we added two classes for these airborne and satellite simulated spectra respectively.
- ii. **Signal processing technique:** We used Verrelst et al. (2015) for grouping reported methods to estimate vegetation characteristics (Table 1). A first categorization delivered two broad groups: physically-based inversion of radiative transfer models and

empirically-based statistical relations. The latter category was further split into univariate regression methods, typically linking one spectral index to a trait of interest, and multivariate regression methods, where more information of the spectrum is used to estimate trait values. The last technique was sub-divided into linear and non-linear models.

iii. **Model evaluation procedure:** Three types of model evaluation strategies are commonly reported in the literature: calibration, validation and resampling. Whereas the calibration $R^2/nRMSE$ expresses the accuracy of a model developed from a training data set, the latter two procedures reflect the models' stability. The validation $R^2/nRMSE$ indicates the ability of a model to estimate trait values of unknown samples in an independent test set. In the resampling $R^2/nRMSE$ the former two expressions are combined by repeatedly building and validating models through iteratively sampling training observations from the entire data set with (e.g. bootstrapping) or without replacement (e.g. K-fold cross-validation) (Efron and Gong, 1983; Olden and Jackson, 2000). In case the type of the reported $R^2/nRMSE$ was not entirely clear, we reached intercoder agreement during the coding procedure.

iv. **Vegetation type:** Although we only investigated herbaceous and shrubby ecosystems, they encompass a large variety of species and plant functional types. We therefore split up the sampling datasets in five major vegetation groups with varying plant life form cover: forbs, grasslands, rangelands, shrublands and wetlands. Shrublands included heathland, chaparral, matorral and moorlands. Rangelands (cerrado, prairie, steppe and savanna) were considered an intermediate vegetation type between grassland and shrubland because they are characterized by a smaller/larger herbaceous and a larger/smaller shrubby vegetation fraction respectively. Following conventional classification systems, wet grasslands were classified separately as wetlands (Latham et

al., 2014; Ramsar Convention Secretariat, 2016; Ramsar COP8 Resolution VIII.11, 2002).

Table 1. Systematic categorization of signal processing methods (based on Verrelst et al. (2015))

Methodological categories	Example techniques
Physically-based algorithms	PROSAIL
Empirically-based algorithms	
Univariate regression methods	Simple ratio indices, normalized differences spectral indices, Red Edge Position (REP) metrics, normalized band depth indices, derivative-based indices
Multivariate regression methods	
Linear models	Stepwise multiple linear regression (SMLR), principal components regression (PCR), partial least squares regression (PLSR), ridge regression (RR)
Non-linear models or Machine learning regression algorithms (MLRAs)	Decision tree learning (DTL) such as Random Forests approach (RF), artificial neural network (ANN), kernel methods such as support vector machine (SVM).

2.3 Data analysis

The central idea of meta-analytical models is to combine the existing evidence of a certain effect to extract general conclusions about it. We defined several effect sizes (*i.e.* several trait estimation accuracies), assuming that the reported accuracies varied across studies (between-studies variance) because they were executed in different circumstances (with specific place, measurement set up, etc.) (Borenstein et al., 2009). In addition, we recognized that accuracies extracted from the same study varied as well (within study-between sample variance) due to the use of various spectral samples and signal processing techniques. By adopting a three-level meta-analytical model we were able to estimate both variances and explore which moderating variables drive accuracy differences within and between studies (Moeyaert et al., 2016; Van den Noortgate et al., 2015).

2.3.1 Effect size

Trait estimation accuracy was typically expressed in terms of the coefficient of determination, and to a lesser extent as the nRMSE in the identified studies. Because meta-analytical three-level models assume normally distributed data (Van den Noortgate et al., 2015), we checked the statistical distribution of the effect sizes for each trait and transformed them in case of non-normality (Mengersen and Gurevitch, 2013). Consequently, we performed a square root transformation to the reported coefficients of determination to convert them into correlation coefficients (r). These results were subsequently transformed to Fisher's Z values (Hedges and Olkin, 1985), defined as

$$Z = \frac{1}{2} \ln \frac{1+r}{1-r} \quad (1)$$

which have an approximate normal distribution with mean zero and variance

$$\sigma_z^2 = \frac{1}{n-3} \quad (2)$$

where n is the sample size.

The nRMSE data distribution approached normality so no transformation was required prior to fitting the meta-analytical models. The variance of the nRMSE records was calculated as (Faber, 1999)

$$\sigma_{nRMSE}^2 = nRMSE \cdot \sqrt{\frac{1}{2 \cdot n}} \quad (3)$$

The Fisher's Z and nRMSE values were used to calculate overall effect sizes and confidence limits, in which each effect size was weighted by the inverse of the variance (Lipsey and Wilson, 2001). For ease of interpretation, the Fishers' Z results were afterwards converted back into coefficients of determination.

2.3.2 Meta-analytical models

For each plant trait we performed a separate meta-analysis. As mentioned before, within each study we often retrieved several estimation accuracies, which cannot be considered to be independent observations. In order to account for this dependency we applied multilevel models (Van den Noortgate et al., 2015, 2013). We assumed three sources of variability: At level 1, effect sizes vary due to a known *sampling variance* (equation 2 and 3); At level 2, effect sizes vary due to the use of different samples within the same study (*between-sample or within-study variance*) and at level 3, effect sizes vary around an overall mean effect size due to the difference between studies (*between-studies variance*). The parameters of the three-level models were estimated using the restricted maximum likelihood estimation procedure implemented in PROC MIXED from SAS (Littell et al., 2006).

First, we estimated the overall estimation accuracy of each trait (null model) and the between-studies and within-study variance. For each trait we fit a three-level random-effects model (REM), in which studies are assumed to be a random sample from a population of studies without a common effect size and samples within studies are considered to be a random sample from a population of samples, rather than being direct replications of each other (Lipsey and Wilson, 2001). The regression equation describing a three-level REM is as follows:

$$X_{jk} = \gamma_{00} + v_{0k} + u_{jk} + e_{jk} \quad (4)$$

The equation shows that X_{jk} , the j^{th} observed (Fisher's Z or nRMSE) effect size from study k , deviates from γ_{00} , the overall mean (Fishers' Z or nRMSE) effect size, due to three random components: v_{0k} , u_{jk} and e_{jk} . The variance of these random components is, respectively, the between-studies variance or variance at the third level (σ_v^2), the within-study (between-samples) variance or variance at the second level (σ_u^2), and the sampling variance or variance at the first level (σ_e^2), that is assumed to be known and it is estimated in advance (equation 2 and 3 so $\sigma_e^2 = \sigma_z^2$ or $\sigma_e^2 = \sigma_{nRMSE}^2$).

Second, we extended the REM's by including each of the potential moderator variables separately (sensor scale, signal processing technique, model evaluation procedure and vegetation type). By doing so, we assumed that the variation around X_{jk} is not entirely random, but that estimation accuracies might differ systematically between the levels of each moderator variable (Viechtbauer, 2007). Here, instead of estimating the overall trait estimation accuracy, we estimated the average accuracy in each of the subgroups defined by the moderators, again by weighting each effect size by the inverse of its variance. These mixed-effect models (MEM's) allowed us to examine whether the unexplained variance present in the null model could be accounted for, at least partially, by the moderator variables. Multiple pairwise differences between the levels of the moderator variables were made, applying the sequential Bonferroni adjustment (Holm, 1979; Rice, 1989). Conclusively, we obtained five models for each trait: one null model and four models with one moderator. In the case of chlorophyll we fitted a sixth model in which we investigated whether significant differences exist between estimates of total chlorophyll, chlorophyll *a* and chlorophyll *b*. Due to a scarcity of records and an unbalanced literature interest in moderator variables, we were unfortunately not able to fit meaningful MEM's for the carotenoid and lignin R^2 datasets, and the nRMSE datasets.

To evaluate the performance of the MEM's compared to the null models, we examined two heterogeneity measurements developed for three-level meta-analysis. Both are based on the rationale that the significance and explanatory power of a moderator variable depends on its ability to reduce the unexplained variance in the null model at either the second or third level.

First, we calculated for each model the level 2 intra-class correlation (ICC) as:

$$ICC_{(2)} = \frac{\hat{\sigma}_u^2}{\hat{\sigma}_u^2 + \hat{\sigma}_v^2} \quad (5)$$

where $\hat{\sigma}_u^2$ and $\hat{\sigma}_v^2$ represent the estimated variance at level 2 and 3 respectively (equation 4) (Cheung, 2014). This index can be interpreted as the proportion of the total between-studies

variance of the effect sizes due to within-study (level 2) variance. By including significant moderator variables at the second level, the heterogeneity at this level $\hat{\sigma}_u^2$ should become smaller, and hence it's portion to the total between-studies heterogeneity $ICC_{(2)}$ should diminish compared to the null-model. The reverse should be noticed if a moderator variable is significant at the third level.

This heterogeneity reduction, from the null model to a MEM, was furthermore quantified in a second metric. More specifically, we investigated to what extent the moderator variables in the MEM's explained the variance at the second and third level in the null model. The larger the explained variance, the more significant the moderator variable will be. The percentage of estimated variance at the second level explained by a moderator variable was calculated as

$$R_{(2)}^2 = 1 - \frac{\hat{\sigma}_u^2(1)}{\hat{\sigma}_u^2(0)} \quad (6)$$

where $\hat{\sigma}_u^2(1)$ and $\hat{\sigma}_u^2(0)$ are the estimated variance at level 2 with (final model) and without (null model) moderator variables respectively (Cheung, 2014). Analogous to equation (6), we assessed the amount of explained variance at the third level by including a moderator variable as

$$R_{(3)}^2 = 1 - \frac{\hat{\sigma}_v^2(1)}{\hat{\sigma}_v^2(0)} \quad (7)$$

where $\hat{\sigma}_v^2(1)$ and $\hat{\sigma}_v^2(0)$ represent the estimated variance at level 3 with and without (null model) moderator variables respectively (Cheung, 2014). Note that we recalculated $\hat{\sigma}_u^2(0)$ and $\hat{\sigma}_v^2(0)$ when moderator levels were excluded due to too few observations.

2.4 Sensitivity and publication bias analyses

Sensitivity analyses were carried out to study the impact of outliers on the meta-analytical results and conclusions (Rothstein et al., 2013). Based on forest plots, we identified possible

outliers in the datasets of the different traits. All analyses were then repeated on the datasets after elimination of the outliers.

Significant results are more likely to be published than non-significant ones (Begg, 1994). We therefore included both published articles and grey literature, such as conference papers. Moreover, we examined the possibility of a publication bias graphically by generating a funnel plot for each trait, on which the standard error was plotted on a reversed scale as a function of effect size (Sterne and Egger, 2001).

3. Results

3.1 Geographical distribution and research trends

The screening and coding of all publications identified resulted in a total of 77 relevant studies of which 41 delivered only R^2 records, 1 delivered only nRMSE records and 35 delivered records for both indicators (Text S1). Together they rendered 569 effect sizes, whereof approximately 70% concerning R^2 statistics, to the meta-analytical models (Table S3, Supplementary data). The geographical coverage of the study sites was mainly Western Europe (Greece, Italy, Netherlands, Spain, Turkey and UK) (e.g. Darvishzadeh et al., 2008b) and North America (Canada and USA) (e.g. Serrano et al., 2000) (Fig. 1). Although both continents showed a uniform research coverage across climate types (Peel et al., 2007), research on the other continents was rather concentrated in particular regions (Australia, Brazil, Chile, China, New Zealand and South Africa) (Garriga et al., 2014; Ramoelo et al., 2013; e.g. Thulin et al., 2012; Wang et al., 2016). In all continents but South America, there was a research bias towards Mediterranean (e.g. Fernández et al., 2015) and temperate ecosystems (e.g. Sanches et al., 2013). South America was the only continent delivering tropical data to our dataset (Brazilian cerrado and pasture in the Amazon) (e.g. Ferreira et al., 2011). Arid ecosystems were limited

to the Great plains of the USA and Canada (e.g. Ling et al., 2014), and the Inner Mongolia
steppe (e.g. Gong et al., 2016).

Figure 1. Locations of the study sites included in the meta-analytical datasets. In the case of greenhouse experiments, the origin of the involved species is indicated on the map. The size of the symbols is proportional to the number of studies that have been carried out at the same location.

Traits which have received most attention can directly be related to productivity: chlorophyll, LAI, nitrogen and phosphorus (Fig. 2, Table S3). In addition, substantial interest was pointed towards water estimation. Studies investigating other pigments than chlorophyll were scarce. We identified five studies estimating carotenoids and only one study predicting anthocyanins content (Garriga et al. 2014). Although vegetation contains many other accessory pigments which influence the spectral reflectance (Ustin et al. 2009), they did not appear in our dataset. We also encountered very few ($n = 4$) studies on lignin estimation.

Figure 2. Number of publications per trait over time

The first publications identified from the literature search dated back to 1998 (Blackburn, 1998; Chen et al., 1998), after which an increasing publication rate was noticeable until 2011 (Fig. 2). This trend corresponded, with a time lag though, to the advancements and proliferation of research in remote sensing instruments and methods. Indeed, approximately ten years after the origin of air- and spaceborne imaging spectrometers, the first applications on trait estimation in herbaceous and shrubby ecosystems appeared in our dataset (Fig. 3) (Chen et al., 1998; Stagakis et al., 2010). Regarding signal processing techniques, univariate regressions were the only models appearing in literature during the first research years, dominated over time (Fig. 4), and mostly involved linear regression models with discrete vegetation indices as independent variable. Linear multivariate techniques have become of major interest over the last decade. Here, the most commonly applied techniques were SMLR (Ramoelo et al., 2011; e.g. Serrano et al., 2002) and PLSR (Darvishzadeh et al., 2008b; Roelofsen et al., 2013). Another noticeable methodological trend was the adoption of non-linear multivariate or machine learning

regression algorithms from 2004 onwards. These mainly included ANN's (Knox et al., 2011; e.g. Mutanga and Skidmore, 2004) and SVM's (Kiala et al., 2016; Wang et al., 2015).

Figure 3. Number of studies per year focusing on each sensor scale. In case that a single publication used the same sensor scale(s) for multiple traits, each trait was considered as a separate study.

Figure 4. Number of studies per year focusing on each signal processing technique. In case that a single publication applied the same signal processing technique(s) on multiple traits, each trait was considered as a separate study.

3.2 Overall trait estimation performance (Model 1)

The overall estimation performance of the studied traits varied between 0.64 and 0.80 for R^2 (Fig. 5; Table 2-4 and S4 – S5), while nRMSE values ranged between 0.09 and 0.26 (Fig. 6). The two most extreme R^2 values ($R^2 = 0.80$ and 0.64 for carotenoids and lignin respectively) were based on few records and publications, and therefore encompassed the largest estimation uncertainty. Also in the case of nRMSE, the poorly encountered carotenoids and lignin records showed least estimation accuracy (overall nRMSE = 0.29 and 0.26 respectively) and highest uncertainty. From the five well-investigated traits in terms of R^2 , LAI models were able to grasp trait variability best ($R^2 = 0.79$). While chlorophyll, phosphorus and nitrogen content showed similar model R^2 values (0.74 – 0.77), their mean nRMSE values differed considerably. More specifically, with an nRMSE of 9% nitrogen turned out to be the most accurately estimated trait compared to all other traits. Models on water content generally had lower precision ($R^2 = 0.69$), but performed well in terms of accuracy (nRMSE = 0.13). Note however that nRMSE values were reported in only one third of the articles addressing water estimation performance, and therefore the mean nRSME value encompassed a relatively large confidence interval (Fig. 6).

Figure 5. Overall mean R^2 and 95% confidence interval of each trait. The code (in format x/y/z) beneath each trait's mean R^2 value indicates the number of effect sizes (x), the number of samples (y) they were based on, and the number of scientific publications (z) they were extracted from.

Figure 6. Overall mean nRMSE and 95% confidence interval of each trait. The code (in format x/y/z) beneath each trait's mean nRMSE value indicates the number of effect sizes (x), the

number of samples (y) they were based on, and the number of scientific publications (z) they were extracted from. Because carotenoid nRMSE was based on one publication only it is not included in this figure.

3.3 Trait estimation performance of different sensor scales (Model 2)

There was a tendency to significance on the effect of sensor scale on the estimation accuracy, expressed as R^2 , of chlorophyll ($p = 0.08$). By accounting for 12.6% of the within-study heterogeneity, the moderator caused the ICC_2 to lower from approximately 32% to approximately 25% (Table 3). Pairwise comparisons indicated that the accuracy of chlorophyll estimation from simulated satellite measurements was higher than the accuracy from real satellite measurements ($p \text{ adj.} = 0.13$). None of the other traits had sufficient data on both real and simulated satellite data to assess possible estimation differences between them. The same was true for airborne data, with an exception for nitrogen, where no significant differences were found (Table 4). Because no evidence of significant differences between estimates from ground-based and airborne/satellite measurements was found, the launch of new space missions for upscaling trait data seems very promising.

3.4 Trait estimation performance of different signal processing techniques (Model 3)

The R^2 models of LAI and chlorophyll showed a statistically significant moderating effect of signal processing technique ($p = 0.002$ and 0.009 respectively) (Table 2 and 3). In the nitrogen dataset this moderator was marginally significant ($p = 0.06$) (Table 4). For all three traits multivariate linear models performed better than univariate models (Fig. 7). In the case of LAI, also multivariate non-linear models provided significantly better results than univariate models. The physically-based model performances for chlorophyll and LAI showed high R^2 variation and were therefore not significantly different from the empirical techniques.

The inclusion of signal processing technique as moderator for LAI estimation accuracy reduced the ICC_2 of the null model almost by half (from 20% to 9.5%) (Table 2). In other words, the moderator variable was capable of explaining almost half of the variance present at the second level in the null model ($R^2_{(2)} = 0.46$). In the chlorophyll and nitrogen null models, a larger part of the total between-studies variance was due to the variance at level 2 ($ICC_2 = 31.7\%$ and 46.4% respectively) (Table 3 and 4). Although approximately 30% of this variability could be accounted for in the chlorophyll dataset, only 8% could be explained in the case of nitrogen.

Figure 7. Mean estimation accuracy and 95% confidence interval of the signal processing techniques for each trait. In brackets the number of effect sizes for each moderator category is specified, the horizontal lines indicate which categories significantly differ (# p adj. $< .1$ and * p adj. $< .01$)

3.5 Additional considerations when evaluating trait estimation performance (Models 4 – 6)

450 From the previous sections it is clear that improvements in accuracy achieved by different
451 sensor scales and signal processing techniques need to be considered in ecological applications.
452 The reliability of these technological and methodological choices might however also be
453 influenced by other moderating variables such as the model evaluation procedure, vegetation
454 type and trait metric.

455 Accuracies obtained through model fitting with the training data set (calibration R^2) were not
456 significantly higher than prediction accuracies of independent trait data (validation R^2). Also
457 resampling procedures gave similar accuracy results. In other words, the predictive power of
458 the traits' estimation models (validation and resampling R^2) turned out to not be significantly
459 different from the calibration results.

460 LAI and chlorophyll estimations showed higher R^2 in shrublands compared to rangelands (p
461 adj. = 0.01 and 0.15 respectively) (Table 2 and 3). In addition, chlorophyll content could be
462 better estimated for shrubland ecosystems than for forbs (p adj. = 0.02) (Table 3). For both traits
463 the $R^2_{(3)}$ revealed that vegetation type accounted for a large part of the heterogeneity present at
464 the third level in the null model: in the LAI dataset 45%, and in the chlorophyll dataset even all
465 variation was explained by including the moderator variable.

466 Although chlorophyll *a* estimation seemed to be more accurate in terms of R^2 , accuracy
467 differences between chlorophyll metrics were not significant (Table 3). Indeed, the moderator
468 variable explained only approximately 3% of the heterogeneity at the third level and none of
469 the heterogeneity at the second level of the null model. None of the tested variables played a
470 significant moderating effect in the phosphorus and water R^2 meta-analytical datasets (Table 4
471 and 6). This was also reflected in the heterogeneity measures of the different models, showing
472 that (almost) none of the variation at the second and third level could be explained by any of
473 the tested moderator variables.

474 **Table 2.** Regression models without moderator (Model 1) and with one moderator (Models 2-5) for **leaf area index**. In models 2 and 5 following
475 moderator levels were excluded due to too few observations: airborne simulations (#1; $R^2 = 0.75$), satellite measurements (#4; mean $R^2 = 0.858$),
476 forb (#2; mean $R^2 = 0.900$), wetland (#4; mean $R^2 = 0.607$).

LEAF AREA INDEX	Regression model statistics						Variance of effect		Heterogeneity measures		
	n	Estimate	SE	F	df (num; den)	p	Level 3	Level 2	ICC_2	$R^2_{(2)}$	$R^2_{(3)}$
Model 1											
Mean estimation accuracy	73	0.793	0.008				0.126	0.032	0.200		
Model 2	68			0.090	1; 16.1	0.770	0.149	0.032	0.178	0.001	0
Airborne	17	0.798	0.026								
Airborne simulations	-	-									
Ground-based canopy	51	0.775	0.016								
Ground-based leaves	-	-									
Satellite	-	-									
Satellite simulations	-	-									
Model 3	73			5.540	3; 49.1	0.002	0.161	0.017	0.095	0.464	0
Multivariate Linear	19	0.858	0.013	Multivariate Linear > Univariate (p adj. 0.003)							
Multivariate Non-linear	11	0.879	0.018	Multivariate Non-linear > Univariate (p adj. 0.004)							
Physically based	10	0.817	0.035								
Univariate	33	0.748	0.010								
Model 4	73			0.290	2; 59.5	0.753	0.129	0.033	0.202	0	0
calibration	32	0.788	0.010								
resampling	19	0.808	0.012								
validation	22	0.787	0.014								
Model 5	67			4.970	2; 26.6	0.015	0.072	0.037	0.341	0	0.445
Forb	-	-									
Grassland	46	0.799	0.010								
Rangeland	10	0.692	0.016	Rangeland < Shrubland (p adj. 0.012)							
Shrubland	11	0.888	0.023								
Wetland	-	-									

477

478 **Table 3.** Regression models without moderator (Model 1) and with one moderator (Models 2-6) for chlorophyll. In model 1 following moderator
479 levels were excluded due to too few observations: airborne measurements (#3; mean $R^2 = 0.556$) and airborne simulations (#2; mean $R^2 = 0.850$).

CHLOROPHYLL	n	Regression model statistics					Variance of effect		Heterogeneity measures		
		Estimate	SE	F	df (num; den)	p	Level 3	Level 2	ICC_2	$R^2_{(2)}$	$R^2_{(3)}$
Model 1											
Mean estimation accuracy	83	0.767	0.008				0.097	0.046	0.321		
Model 2	78			2.360	3; 47.1	0.083	0.132	0.045	0.255	0.126	0
Airborne		-	-								
Airborne simulations		-	-								
Ground-based canopy	60	0.786	0.013								
Ground-based leaves	6	0.679	0.040								
Satellite	6	0.609	0.067	Satellite < Satellite simulations (p adj. 0.130)							
Satellite simulations	6	0.871	0.043								
Model 3	83			5.910	2; 23.5	0.008	0.130	0.032	0.199	0.299	0
Multivariate Linear	28	0.836	0.014	Multivariate Linear > Univariate (p adj. 0.007)							
Multivariate Non-linear		-	-								
Physically based	9	0.780	0.052								
Univariate	46	0.724	0.012								
Model 4	83			1.630	2; 41.5	0.101	0.101	0.045	0.308	0.020	0
calibration	49	0.788	0.009								
resampling	8	0.754	0.018								
validation	26	0.714	0.013								
Model 5	83			5.440	4; 12.7	0.009	0.095	0.026	0.219	0.423	0.027
Forb	18	0.721	0.022	Forb < Shrubland (p adj. 0.018)							
Grassland	26	0.771	0.017								
Rangeland	6	0.362	0.097	Rangeland < Shrubland (p adj. 0.130)							
Shrubland	25	0.878	0.020								
Wetland	8	0.687	0.052								
Model 6	83			0.730	2; 74.1	0.483	0.095	0.047	0.329	0	0.020
Total chlorophyll	51	0.759	0.008								
Chlorophyll <i>a</i>	16	0.809	0.016								
Chlorophyll <i>b</i>	16	0.765	0.016								

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482 **Table 4.** Regression models without moderator (Model 1) and with one moderator (Models 2-6) for **nitrogen**. In model 1 and 5 following moderator
483 levels were excluded due to too few observations: satellite simulations (#1; $R^2=0.830$) and shrubland (#3; mean $R^2 = 0.723$).

NITROGEN	n	Regression model statistics					Variance of effect		Heterogeneity measures		
		Estimate	SE	F	df (num; den)	p	Level 3	Level 2	ICC_2	$R^2_{(2)}$	$R^2_{(3)}$
Model 1											
Mean estimation accuracy	129	0.740	0.004				0.074	0.064	0.464		
Model 2	128			1.360	3; 105	0.258	0.077	0.063	0.448	0.034	0
Airborne	36	0.682	0.008								
Airborne simulations	7	0.784	0.021								
Ground-based canopy	79	0.755	0.004								
Ground-based leaves	6	0.721	0.027								
Satellite	-	-	-								
Satellite simulations	-	-	-								
Model 3	129			2.850	2; 112	0.062	0.080	0.059	0.425	0.079	0
Multivariate Linear	68	0.766	0.005	Multivariate Linear > Univariate (p adj. 0.058)							
Multivariate Non-linear	11	0.762	0.015								
Physically based	-	-	-								
Univariate	50	0.683	0.006								
Model 4	129			0.190	2; 112	0.831	0.074	0.065	0.469	0	0
calibration	62	0.732	0.005								
resampling	26	0.757	0.008								
validation	41	0.737	0.007								
Model 5	126			0.340	3; 17.9	0.798	0.090	0.062	0.409	0.014	0
Forb	8	0.735	0.095								
Grassland	47	0.762	0.008								
Rangeland	61	0.702	0.012								
Shrubland	-	-	-								
Wetland	10	0.776	0.051								

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3.6 Sensitivity analysis and publication bias

For three traits, an outlier in the R^2 datasets could be identified (Fig. 8). In the case of LAI, it concerned an extremely low calibration R^2 of a linear univariate model fit on airborne data in a rangeland (Lee et al. 2004). Both the nitrogen and phosphorus outlier originated from Kawamura et al. (2009) and concerned an extreme high calibration R^2 of a PLSR model fit on ground-based canopy measurements of a grassland. In the nRMSE trait datasets there was no indication of outlying records (Fig. S1).

By removing the outliers, the overall R^2 of 0.79 for LAI increased to 0.80 (standard error 0.006). The mean estimation accuracy for phosphorus and nitrogen on the contrary decreased from 0.76 and 0.74 to 0.74 (standard error 0.005) and 0.73 (standard error 0.002), respectively. In all three cases, the resulting pool of effect sizes was considerably more homogeneous compared to the original databases. More specifically, eliminating outliers reduced the total between-studies heterogeneity, due to level 2 and level 3 variability, by half in the nitrogen dataset, and by third in the other two trait datasets. The regression models including a moderator variable yielded a pattern of results that is similar to our previous results, with the same moderator variables reaching significance. It should be noted that now both rangelands and grasslands showed lower LAI estimation accuracies compared to shrublands (p adj. 0.02 and 0.14, respectively).

A visual inspection of the funnel plots did not indicate the presence of publication bias in the R^2 datasets, with all plots showing a more or less symmetrical distribution of effect sizes (Fig. S2). Because nRMSE values are per definition correlated with standard errors, the use of funnel plots was not appropriate for detecting possible publication bias in these datasets. Given that almost half of the identified studies reported both indicators (more specifically 35 out of 77 studies), and given that there was no publication bias present in the R^2 data, it is unlikely that publication bias exists in the nRMSE data.

Figure 8. Forest plot: observed Fisher's Z effect sizes with their 95% confidence interval, ordered by trait and by magnitude of the effect size. The overall Fisher's Z effect size for each trait is indicated and accompanied by a dashed vertical line.

4. Discussion

This meta-analysis of 77 studies demonstrates the potential of hyperspectral remote sensing data for the functional characterization of grass- and shrubland vegetation. Generally high estimation accuracies can be reached following the recommendations of Richter et al. (2012), but this strongly depends on the trait to be quantified, and is influenced by methodological and technological choices. We discuss these topics here and mention research trends whenever relevant and informative for the context.

4.1 Overall trait estimation performance in grass- and shrubland ecosystems

Chlorophyll and carotenoid concentrations can be estimated with high R^2 and reasonable nRMSE. Our R^2 values are in accordance with Huang et al. (2015), who summarized pigment estimation accuracies over a broad range of vegetation types. There are two reasons why these pigments can be retrieved so well. First, being part of the photosynthetic antenna or light-harvesting complex, they show strong absorbance properties of light in the visible region (Curran, 1989; Ustin et al., 2009). Secondly, because of their particular spectral behaviour, and given their important physiological roles, leaf pigments are one of the most well-studied traits in the remote sensing community (we identified 16 relevant studies rendering 82 records). Surprisingly, pigments are not included in guidelines on functional trait measurement (Knevel et al., 2005; Pérez-Harguindeguy et al., 2013), and therefore generally not involved in functional ecology studies. Hyperspectral measurements of pigments concentrations could however deliver promising information on the spectrum of plant function (Díaz et al., 2015; Wright et al., 2004), and therefore form a basis for monitoring ecological processes. Notwithstanding the progress in understanding pigment effects on plant spectral properties, the majority of research has been dedicated towards the estimation of chlorophyll content, more specifically the retrieval of total chlorophyll content. This is due to the difficulty in resolving the spectral overlap of various pigments' absorption features and their high degree of autocorrelation (Chappelle et al., 1992; Ustin et al., 2009).

540 With a similar estimation R^2 as chlorophyll, also phosphorus and nitrogen can readily be
 541 estimated in grass- and shrubland ecosystems. The fact that our nitrogen estimation R^2 is only
 542 slightly higher than reported earlier (Homolová et al., 2013), nRMSE is lowest of all traits and
 543 below previously reported average values (Homolová et al., 2013), and the remarkably large
 544 amount of studies dedicated to its estimation, suggests that its absorption characteristics are
 545 well-understood today. Nitrogen is mostly tied up in cytoplasmic enzymes, especially Rubisco,
 546 involved in the carbon fixation process of photosynthesis (Chapin 1987; Elvidge, 1990), and to
 547 a lesser extent also allocated to the chlorophyll molecule itself (Evans, 1983). Its concentrations
 548 are therefore correlated both with spectral patterns in the NIR and SWIR region associated with
 549 vibrations of the N-H and C-H bonds in proteins (Curran, 1989; Smith et al., 2003), and
 550 channels in the visible region, where pigments play a major role (Kokaly et al., 2009).
 551 Regarding phosphorus estimation, substantial advances have been made during the past few
 552 years as we obtained a much higher retrieval R^2 and a substantially lower nRMSE than
 553 Homolová et al. (2013), who based their result on very few observations (7 records extracted
 554 from 4 studies). Similar to nitrogen estimation, bands in both the visible and SWIR region seem
 555 to be important for the estimation of phosphorus concentration (Mutanga and Kumar, 2007).
 556 Estimation of grass and shrub water content turned out to be considerably less precise than
 557 pigments, nitrogen and phosphorus in terms of R^2 , but spans the same range of accuracy when
 558 looking at nRMSE. Although its direct effects on the spectral reflectance, caused by the
 559 absorption properties of water itself, are reasonably straightforward (Carter, 1991; Curran,
 560 1989), the retrieval is complicated by indirect effects of other plant biochemical properties as
 561 well as leaf and canopy structure that covary with water status (Danson et al., 1992; Ollinger,
 562 2011). At the canopy level, the situation is even more convoluted by atmospheric water vapour
 563 effects (Feilhauer et al., 2015). Radiative transfer models have proven to be very useful for
 564 disentangling these covarying properties (Jacquemoud, 2000; Jacquemoud et al., 2009), and

hence provide a strong basis for developing and optimising vegetation indices with minimal sensitivity to differences in soil brightness, and illumination and observation geometry (Ceccato et al., 2002a, 2002b). However, even recent attempts at spectral band selection indicate that water content remains a challenging trait to estimate (Feilhauer et al., 2015). Despite the large amount of vegetation indices developed and tested – it is remarkable that the big majority of our water records are based on univariate regressions – our analyses delivered lower R^2 and nRMSE values than generally observed in forests (Asner et al., 2011; Asner and Martin, 2011; Gao and Goetz, 1995). The studies involved in our meta-analysis showed that relationships between water content and remotely sensed measures can be strongly affected by vegetation architecture and the presence of non-photosynthetic components such as soil and senesced vegetation (Serrano et al., 2000), which particularly during the dry season lead to estimation problems (Numata et al., 2008; Rahman and Gamon, 2004). This might explain why also in agricultural ecosystems a wide range of accuracies has been reported (e.g. Feng et al., 2017; Zhang and Zhou, 2015).

Finally, lignin showed the lowest estimation R^2 , highest nRMSE, and largest confidence intervals. Also in forest ecosystems, a wide variety of performance values has been reported, generally of lower accuracy and with higher estimation error when compared to the estimation of pigments, nitrogen, phosphorus and water content (Asner and Martin, 2011; Martin and Aber, 1997; McManus et al., 2016). This has been partly assigned to the difficulty of quantifying lignin in the laboratory due to its heterogeneous chemical composition (LaCapra et al., 1996). Moreover, the polymer is closely intertwined with cellulose and other polysaccharides, having overlapping spectral absorption properties (Kokaly et al., 2009). On the one hand, these complexities provide a reason as to why only few researchers have focused upon the estimation of lignin (and cellulose) content in both forest, agricultural and grass- and shrubland ecosystems. On the other hand, they form a motivation for a more extensive

investigation in remote techniques as an alternative to labour intensive laboratory analyses for the quantification of these components.

From a structural perspective, only leaf area index has been a central theme in grass- and shrubland research, and it turned out to be accurately retrievable from hyperspectral data. Similar R^2 and nRMSE values have been reported in forests (Banskota et al., 2013; Schlerf and Atzberger, 2006) and agro-ecosystems (Gupta et al., 2006; Haboudane et al., 2004). Although hyperspectral data has also proven successful in the estimation of grass and shrub SLA or LMA (Ball et al., 2015; Casas et al., 2014), and grassland vegetation height (Capolupo et al., 2015), these applications are unique. Also in forests (Ali et al., 2017; Asner et al., 2015) and agro-ecosystems (Ecarnot et al., 2013) hyperspectral LMA/SLA quantification studies remain limited and inconsistent results have been reported (Homolová et al., 2013). Because these plant morphological properties are essential traits in many ecological studies – they are relatively easy to measure and indicate fundamental trade-offs in plant strategies related to light interception, competitive vigour and investment in resources (Poorter et al. 2009; Díaz et al. 2015) – they urgently deserve more attention by the remote sensing community. It should be noted however that active remote sensing technology, such as light detection and ranging (LiDAR), high-density laser scanning and synthetic aperture radar (SAR), are more common and promising to accurately assess individual plant and vegetation structural traits (Abelleira Martínez et al., 2016; Lausch et al., 2016), even in low-stature vegetation. Indeed, accurate results have been reported for the active sensing of herbaceous ($R^2 = 0.74 - 0.88$; (Straatsma and Middelkoop, 2007)) and shrub vegetation height ($R^2 = 0.58 - 0.94$; (Glenn et al., 2011; Vierling et al., 2012)).

4.2 Trait estimation performance of different sensor scales

In the past 20 years, a growing body of literature has demonstrated the successful use of hyperspectral data for trait quantifications in grass- and shrubland ecosystems across spectral measurement scales: from leaf to whole-plant reflectance spectra collected in the field or in the laboratory, to vegetation canopy reflectance measurements made by air- and spaceborne imaging spectrometers. Contrary to the remote sensing history of forest and agro-ecosystems (Huang et al., 2015; Majeke et al., 2008), only few records in our meta-analysis involved leaf level reflectance measurements. A reason for this might be that the relatively small/narrow size of most herbaceous and grass species leaves complicates spectral measurements at this detailed scale. Furthermore, from a monitoring and management perspective it is generally more desirable to have spatially explicit biochemical and structural content at one's disposal. These aspects explain the literature focus on canopy models in which traits are directly being linked to canopy spectral data measured in the field or by air- or spaceborne sensors.

Canopy level measurements however include some challenges. The presence of multiple plant functional types varying in terms of growth and resource allocation strategies (Golluscio and Sala, 1993; Kalacska et al., 2015) could explain why trait estimations in rangelands generally involve smaller accuracies. This hypothesis is supported by Ball et al. (2015), who were not able to spectrally capture the differences in trait values between various life forms in a cerrado ecosystem. In addition to the small-scale heterogeneity in species and functional composition, remote sensing applications in grass- and shrubland ecosystems are often complicated by the presence of a high fraction of non-photosynthetic vegetation and soil (He and Mui, 2010). This could motivate why chlorophyll (and nitrogen) estimations based on satellite (and airborne) simulations are better than those based on real satellite (and airborne) measurements. Indeed, ground-based spectra which are used for the simulation of airborne or satellite spectral equivalents usually encompass green vegetation patches or healthy leaves, and therefore do not always represent the real situation in the field. Additionally it should be noted that the presence

638 of non-photosynthetic components impacts the definition and traditional field measurements of
639 LAI. Most frequently the plant area index (PAI) (Chen et al., 1997), including both
640 photosynthetic and non-photosynthetic components, rather than green LAI was characterized
641 in the identified studies (e.g. Darvishzadeh et al., 2008b). Another source of spatial variation of
642 grassland vegetation can be attributed to topographic effects, which determine the distribution
643 of soil water content, solar radiation and soil organic community (He et al., 2006; Phillips et
644 al., 2012). The optimal pixel size of remotely sensed data for studying functional vegetation
645 properties in these ecosystems is therefore largely dependent on the scale of these spatial
646 patterns (Curran and Atkinson, 1999; Lobo et al., 1998). A reason why relations might become
647 stronger at coarser resolution is that external factors causing fine-scale variation get filtered out
648 (Davidson and Csillag, 2001). Although He et al. (2006) could better estimate grassland LAI
649 when upscaling original 3 m resolution images to a coarser pixel size of 30 m, Rahman et al.
650 (Rahman et al., 2003) proposed to limit maximum pixel size to 6 m in order to still be able to
651 adequately capture variations in functional properties. The trade-off between smoothing fine-
652 scale disturbances and preserving important spatial detail, dependent on plant functional
653 diversity and the effect of topography, provides an explanation as to why we did not observe
654 significant differences between estimations based on ground-based canopy, airborne and
655 satellite measurements. These results are thus promising for future generation airborne and
656 satellite missions, and large-scale ecological applications. Apart from these general findings, it
657 should be noted however that a full intercomparison of all sensor scales was not feasible for
658 none of the investigated traits due to a research lag on the use of air- and spaceborne
659 measurements. Although the monitoring of seasonal trait changes is a relevant topic in
660 biodiversity science (e.g. Knox et al., 2012; Sanches et al., 2013), we noticed moreover that
661 only 11 studies explicitly investigated trait estimation accuracies over time. Due to the limited
662 temporal coverage of current satellites and high costs of airborne field campaigns, these studies

encompassed mainly spectral time-series of ground-based canopy measurements. With the development of UAV's and compatible hyperspectral sensors (Capolupo et al., 2015; Mitchell et al., 2012), and coordinated initiatives for integrating proximal and remote sensing (Scholes et al., 2012; Turner, 2014), research on the stability and resilience of herbaceous ecosystems will advance, and global patterns and dynamics of plant functional diversity in grass- and shrublands may be better monitored through time.

4.3 Trait estimation performance of different signal processing techniques techniques

Trade-offs also exist when evaluating different signal processing techniques. Multivariate regression turned out to have the greatest potential, in terms of R^2 , for retrieving LAI, chlorophyll and nitrogen content. Moreover multivariate methods have proved to be promising for estimating grassland biomass (e.g. Ali et al., 2014; Clevers et al., 2007; Marabel and Alvarez-Taboada, 2013) and other chemical traits important for forage quality (e.g. Biewer et al., 2009; Capolupo et al., 2015). The potential to make use of the complete spectral information is often put forward as the reason why multivariate models outperform univariate regressions, where only a few spectral bands are used for calculating vegetation indices. The latter models tend therefore to be more noise-sensitive as compared to full-spectrum ones (Atzberger et al., 2010; Baret and Guyot, 1991). The possibility of adding multiple bands to a multivariate regression holds some risks, however, because it may lead to model overfitting (Lee et al. 2004). Nevertheless, during the last decade substantial progress has been made in the field of multivariate modelling, which is also reflected in its increasing application in functional grass- and shrubland remote sensing over time. Similarly, the exploration of different multivariate techniques is up and coming in forests (e.g. Coops et al., 2003; Huang et al., 2004; Majeke et al., 2008) and croplands (e.g. Atzberger et al., 2010; Hansen and Schjoerring, 2003). Multivariate methods are considered state-of-the-art for operational mapping applications (Verrelst et al., 2015). Although our results suggest that linear and non-linear multivariate

models perform equally well, the appropriate choice should be made in function of the ecosystem's characteristics under investigation. Whereas linear models are convenient in situations where vegetation is not dense (e.g. Marabel & Alvarez-Taboada 2013), non-linear models should be adopted in denser situations (Kiala et al., 2016) because they can better deal with spectral saturation, among others appearing at higher biomass density (Axelsson et al., 2013; Clevers and Kooistra, 2012).

5. Conclusion and final remarks

The biophysical and -chemical trait composition of vegetation provides crucial insights into its condition and functioning. During the last few decades, the remote sensing community has placed great emphasis on the development of sensor technology and signal processing techniques for functional trait quantification. Through documenting the scope, geographic distribution and history of hyperspectral sensing in support of functional ecology in grass- and shrublands, and assessing trait estimation accuracy, we have identified some knowledge gaps and promising pathways for improvements.

Although hyperspectral remote sensing forms a promising data source for estimating a suite of functional properties in herbaceous and shrubby ecosystems, especially leaf morphological properties and biochemical traits which are not growth-related remain underexplored. Important structural traits such as SLA and LDMC, and vitality and longevity compounds such as water, lignin and cellulose need more attention. Furthermore, it should be noted that the majority of screened studies were carried out in Mediterranean and temperate climates. In order to come at a global remote sensing of plant functional types (Schweiger et al., 2017; Ustin and Gamon, 2010; Wullschleger et al., 2014) and functional diversity (Jetz et al., 2016) more emphasis should be put on grass- and shrubland ecosystems in arid and tropical areas.

Our study showed that the computational complexity of multivariate models is worth the effort in terms of R^2 when quantifying LAI, chlorophyll and nitrogen. Because research on these three traits seemed to be in a mature stage – they have received considerably more attention compared to other functional properties and involve highest estimation accuracy – we expect that multivariate techniques will become more popular and have the potential to improve estimation accuracies of other traits as well.

Finally, our study indicated that airborne and satellite missions encompass great potential for detecting functional traits in grass- and shrublands. Although the capabilities of these platforms in grass- and shrublands are not (yet) fully explored, our meta-analysis provides optimistic outlooks for recent initiatives urging a global biodiversity observatory (Jetz et al., 2016; Scholes et al., 2012), and pleading satellite remote sensing essential biodiversity variables (Paganini et al., 2016; Pettorelli et al., 2016).

Despite the gathered insights, we would like to stress the importance of proper publication standards in order to facilitate future meta-analytical reviews. Due to a lack of statistical information regarding our second and third screening criteria (*i.e.* reporting of goodness-of-fit-statistics and sample size) in many studies, we were not able to execute a more comprehensive inter-comparison of the various moderator levels. Although it is getting widely recognized that model performance should be evaluated based on multiple indices, there was moreover a large publication bias towards R^2 records in the collected set of publications. Besides it was not always clear if reported indicators represented calibration, resampling or validation accuracy. In those cases, we reached intercoder agreement upon the model evaluation procedure during the coding procedure. It is therefore highly recommended that statistical analyses in primary research are always accompanied with clear details on the input dataset and output specifications. These actions will support future meta-analytical reviews, which can provide

736 essential insights in technological advancements, reveal knowledge gaps and highlight potential
737 capabilities of remote sensing.

738

739 **Supplementary information**

740 Supplementary material – Supporting figures, tables and text

741 Supplementary data – Trait datasets for meta-analysis: Summary of characteristics of
742 hyperspectral studies on trait estimation in grass and herbaceous ecosystems conducted by other
743 researchers.

744

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1412 **List of figure captions**

1413 **Figure 1.** Locations of the study sites included in the meta-analytical datasets. In the case of
 1414 greenhouse experiments, the origin of the involved species is indicated on the map. The size of
 1415 the symbols is proportional to the number of studies that have been carried out at the same
 1416 location.

1417 **Figure 2.** Number of publications per trait over time

1418 **Figure 3.** Number of studies per year focusing on each sensor scale. In case that a single
 1419 publication used the same sensor scale(s) for multiple traits, each trait was considered as a
 1420 separate study.

1421 **Figure 4.** Number of studies per year focusing on each signal processing technique. In case that
 1422 a single publication applied the same signal processing technique(s) on multiple traits, each trait
 1423 was considered as a separate study.

1424 **Figure 5.** Overall mean R^2 and 95% confidence interval of each trait. The code (in format x/y/z)
 1425 beneath each trait's mean R^2 value indicates the number of effect sizes (x), the number of
 1426 samples (y) they were based on, and the number of scientific publications (z) they were
 1427 extracted from.

1428 **Figure 6.** Overall mean nRMSE and 95% confidence interval of each trait. The code (in format
1429 x/y/z) beneath each trait's mean nRMSE value indicates the number of effect sizes (x), the
1430 number of samples (y) they were based on, and the number of scientific publications (z) they
1431 were extracted from. Because carotenoid nRMSE was based on one publication only it is not
1432 included in this figure.

1433 **Figure 7.** Mean estimation accuracy and 95% confidence interval of the signal processing
1434 techniques for each trait. In brackets the number of effect sizes for each moderator category is
1435 specified, the horizontal lines indicate which categories significantly differ (# p adj. < .1 and
1436 * p adj. < .01)

1437 **Figure 8.** Forest plot: observed Fisher's Z effect sizes with their 95% confidence interval,
1438 ordered by trait and by magnitude of the effect size. The overall Fisher's Z effect size for each
1439 trait is indicated and accompanied by a dashed vertical line.