

Cover vs. biomass sampling in grassland vegetation plots

Vegetationsaufnahmen im Grünland: Deckungsschätzung vs. Biomassewägung

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Abstract

Vegetation ecologists use a wide range of importance (“abundance”) measures for plant species in vegetation plots, including percentage cover, ordinal cover scales, frequency and fractional biomass. Resurvey studies and analyses of heterogenous data from large vegetation-plot databases need to deal with data sampled with different approaches, yet very little is known about how these approaches relate to each other. For the Square Foot Project, in which hundreds of historic grassland plots in Switzerland of 0.09 m² size were resurveyed after having been originally sampled via biomass harvest, we had the challenge that the historical method was too time-consuming for our study and thus had to resort to careful cover estimation in percent. However, we used both methods to sample 40 such plots representative of the grasslands of Switzerland and compared the results. We found that with biomass-based species determination, an average of 0.9 additional species (4.6%) per plot were found compared to cover-based sampling. Graminoids were three times more likely to be overlooked than forbs. Fractional cover was well related to fractional biomass with an allometric (power-law) function, with an exponent of 0.6 for all species combined, while graminoids and forbs showed clear differences in function parameters when analysed separately. Generally, our overlooking probabilities were much lower than in other comparable studies, which might be due to the very small plot size or to the careful sampling with percentage estimates. Our allometric functions allow reliable transformations between fractional biomass and fractional cover in temperate European grasslands. We recommend the development of further such empirical functions for other regions and ecosystems.

Keywords: abundance, allometric function, biomass, cover estimation, grassland, observer error, sampling methodology, species richness, Square Foot Project, vegetation plot

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Vegetation-plot records (relevés) are the most widespread sampling method in vegetation ecology. They involve recording all species within a defined sampling area (plot), usually combined with a measure of species importance, sometimes laxly called “abundance” (van der Maarel & Franklin 2013). There is a wide range of such importance measures for plant species, most importantly cover (fractional area that is covered by the vertical projection of the aboveground parts of a species), abundance s.str. (number of individuals of a species per unit area), frequency (fraction of equally sized subplots in which the species occurs) and biomass per unit area (usually based on above-ground dry mass) (Knapp 1971, Mueller-Dombois & Ellenberg 1974, Dierschke 1994, van der Maarel & Franklin 2013). All these importance values can be measured or estimated, and they can be either given directly in percent or on an ordinal scale (see Dengler & Dembicz 2023). Which variant of which importance measure is used strongly depends on the tradition in the respective school/sub-discipline of vegetation science.

Generally, in vegetation science, cover is the prevailing importance measure, as direct cover estimates in percent, in an ordinal cover scale or in a combined cover-abundance scale (like most variants of the Braun-Blanquet scale; see Dengler & Dembicz 2023). For example, in the global vegetation-plot database sPlot (Bruelheide et al. 2019), 96% of all plots used some form of cover information, 66% thereof different variants of the Braun-Blanquet cover-(abundance) scale and 15% an estimation in percent. The popularity of cover-based measures rests on their relatively high information content, combined with the low amount of time needed to record them with considerable reliability. By contrast, biomass, either measured or estimated, could be considered an even better measure of the real ecological importance of a species in a community, while at the same time being more challenging to record. Estimating the biomass or biomass fraction in the field is far more demanding than estimating cover since it involves three dimensions instead of two and depends on the density of plant tissues, likely making it less reproducible. Measuring biomass, on the other hand, can be highly precise, but it is destructive (biomass harvest needed) and extremely time consuming. Therefore, biomass is rarely used as an importance measure (absent among the > 1 million plots in sPlot 2.1; Bruelheide et al. 2019) and largely restricted to agronomic purposes or experimental settings (Kreyling et al. 2011).

Challenges arise from the fact that there are so many different ways to quantify species importance in a plot (e.g. 57 methods included in sPlot; Bruelheide et al. 2019), while it becomes more and more relevant to combine different measures in a single analysis. This is true for broad-scale analyses using large vegetation-plot databases (e.g. Chytrý et al. 2016, Bruelheide et al. 2019) as well as resurvey studies of vegetation plots (see Kapfer et al. 2017). In overarching studies with multiple plant importance measures all values are usually scaled to relative importances (“relative abundances”) p_i , with p_i of species i being the importance value for that species divided by the sum of the importance values of all species (Bruelheide et al. 2019); yet this assumes that p_i for different importance measures is equivalent. In resurvey studies, one theoretically could repeat the old sampling method, but if this was biomass, this might be too time consuming for present-day project budgets. Thus, there is a clear need to understand how different importance measures can approximately be translated into each other. Since there are only few studies that have established such translations for specific situations (Axmanová et al. 2012, Lisner & Lepš 2020, Monzingo et al. 2022), more studies are necessary to achieve better generality. Moreover, the choice of method does not only influence the importance measure and its reliability (e.g. Dengler &

Dembicz 2023) but can also have effects on the recorded species richness. While there are some studies that have quantified the number of overlooked species when sampling the same plot in the same year with the same method by different researchers (e.g. Klimeš et al. 2001, Boch et al. 2022, see also review by Morrison 2016), we are aware of only one study that did this in comparison of different methods (Lisner & Lepš 2020).

We faced these issues in the Square Foot Project (www.zhaw.ch/squarefoot; Riedel et al. 2023). This project aims at quantifying the vegetation change in Swiss grasslands over more than a century, based on a resurvey in 2021 and 2022 of 580 0.09-m² plots originally sampled from 1884 to 1931 (e.g. Stebler & Schröter 1887, see Riedel et al. 2023). The plots were historically recorded using biomass (fractions), a method that we could not repeat for all plots due to time constraints. Instead, we conducted the resurveys with percentage cover estimates, while testing the differences between the results using the old (biomass weighting) and the new (cover estimation) method for a representative subset of the plots. While this study was mainly done to inform forthcoming publications of the Square Foot Project, we realised that such comparisons of different methods of species importance assessment are so rare in the literature that our results might be of more general relevance. Specifically, we asked the following questions in relation to visual cover estimation in percent vs. the measurement of dry aboveground biomass: (1) How are these two importance measures related to each other? (2) Does the number of detected species differ between the two methods? (3) Are the patterns found for (1) and (2) dependent on growth form? (4) How can these results best be accounted for in a study that combines samples with the two different methods?

2. Methods

2.1 Study sites

The 40 study plots were located in Swiss grasslands covering an elevational gradient from 435 to 2216 m a.s.l. (Fig. 1) and included different moisture and nutrient levels. The observed species richness of the 0.09-m² plots in the field ranged from 6 to 38 species, with a mean of 18.8 species. The term “species” refers here to all terminal taxa, including aggregates and genera without further determination. In around half of the plots, most of the plants were still in vegetative stage, while in the other half, most of the plants were flowering.

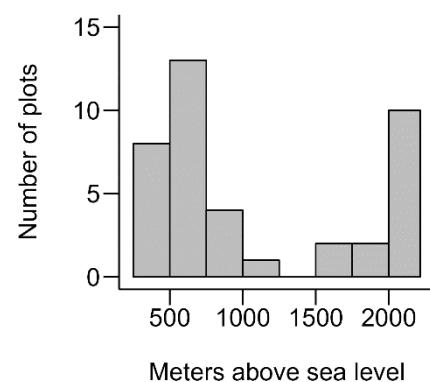


Fig. 1. Distribution of the vegetation plots along the elevational gradient.

Abb. 1. Verteilung der Aufnahmeflächen in Abhängigkeit von der Meereshöhe.

2.2 Historical sampling method and resurvey method

To delimit the recording surface to the Square Foot standard (Riedel et al. 2023), we drove a 30 cm × 30 cm metal frame into the ground, keeping all parts of the rooting plants within the square (Fig. 2). In a first step, the vascular plant species inside the frame were identified and the cover of each species was estimated as precisely as possible in percent.



Fig. 2. Metal frame of 0.3 m × 0.3 m size that was driven a few centimetres into the soil to cut out the sod.

Abb. 2. Metallrahmen von 0,3 × 0,3 m Grösse, der einige Zentimeter in den Boden gedrückt wurde, um dann die Sode unterhalb abzustechen.

Corresponding to the historic method (Stebler & Schröter 1887), we then cut this 0.09-m² square a few centimetres below the soil surface. The isolated sod was then taken to the laboratory, where the plants were cut as close to the soil surface as possible, separated, identified and sorted by species. In cases where weather conditions and the available time allowed, this work was done directly in the field. Placed in a microperforated bag by species, the plants were dried for 24 hours at 60 °C and then weighed on a precision balance.

The identification of the species in the field and the cover estimation were done by S.R (37 plots), S.W (3 plots) and one other observer (1 plot), often supported by O.B. The biomass measurements, including identification and sorting, were carried out by O.B with the help of species lists from the field. Plant nomenclature follows the current Swiss checklist (Juillerat et al. 2017).

2.3 Statistical analyses

All statistical analyses were performed in R version 4.3.1 (R CORE TEAM 2023).

2.3.1 Differences in species richness between the field and the lab sampling

To test if the species richness of a plot recorded in the field was different from the one recorded in the lab, we ran paired *t*-tests. We did this comparison for all species combined and separately for the graminoids (*Poaceae*, *Cyperaceae*, *Juncaceae*) and the forbs (all other families, including dwarf shrubs and tree seedlings).

To determine the overlooking probability of a species in the field, we used a logistic regression with overlooking probability as the response variable and fractional dry mass as predictor. In the binomial distribution, we coded species recorded in the lab and in the field as 1 and species only recorded in the lab as 0, while species found only in the field were disregarded.

2.3.2 Translation from biomass to percent cover

To translate biomass [g] to cover [%], we ran linear mixed models with a random slope and a random intercept, and the species identity as random factor. In biology, the relationship between two quantities of an organism can be expressed as an allometric equation (power law equation) (West et al.

1997, Chen & Shiyomi 2019). To be able to fit a linear model, we therefore transformed the dependent estimated cover and the independent biomass using the logarithm with base 10. With the function “lmer” of the package lmerTest (Kuznetsova et al. 2017) the model was specified as follows:

$$lmer(\log_{10}(\text{Cover}) \sim \log_{10}(\text{Dry mass}) + (\log_{10}(\text{Dry mass}) / \text{Species})$$

The function “r2_nakagawa” of the “performance” package (Lüdecke et al. 2021) was used to calculate the marginal and conditional R^2 . The marginal R^2 considers only the variance explained by the fixed effect, whereas the conditional R^2 also considers the random effect (Nakagawa et al. 2017). The linear mixed model (lme) was calculated with all species for the measured biomass [g] (independent variable) and the estimated cover [%] (dependent variable) and/or for the fractions thereof, resulting in four different combinations:

Fractional estimated cover [%] and Fractional measured biomass [g]
Fractional estimated cover [%] and measured biomass [g]
Estimated cover [%] and Fractional measured biomass [g]
Estimated cover [%] and measured biomass [g]

For the best model (fractional estimated cover [%] ~ fractional biomass [g]), we additionally ran separate models (1) for the graminoids and the forb species (2) with and (3) without rosettes, assuming that the different structure of these three growth forms might affect the allometric function. The assignment of the species to the category rosette or non-rosette was based on our personal knowledge (see the Supplement E1 for the complete species list with the assigned category).

3. Results

3.1 Time required for the two methods

The method “cover estimation” required on average around one hour per plot to identify the plant species in the field and estimate their cover with high precision. By contrast, the method “biomass” required around three hours per plot for cutting, sorting and determining the plant species. Another hour was needed to weigh the dried specimens, bringing the total time necessary for this method to about four hours, excluding drying time.

3.2 Species richness and detection probability

A total of 796 species observations in 40 plots were recorded in the field and the lab, representing 231 species or aggregates, 125 genera and 42 families. *Poaceae* (235) was the most frequent family followed by *Asteraceae* (84) and *Fabaceae* (68). In all 40 plots, 46 species were observed for plots in the lab that had not been identified in the field (5.8%; Table 1). Conversely, 10 species observations from the field could not be confirmed in the lab (1.3%; Table 2).

According to the paired *t*-tests, we found on average 0.9 species or 4.6% less in the field (18.8) than in the lab (19.7, $p < 0.001$). The mean difference was higher for graminoids (0.6 species, $p < 0.001$) than for forbs (0.3 species, $p = 0.039$) (Fig. 3).

The probability of not recording a species in the field that later was found in the lab depended on its importance value expressed as fractional biomass, but also varied between graminoids and forbs (Table 3, Fig. 4).

Table 1. Species that remained undetected when estimating the cover in the field but were identified in the lab. The values are expressed in absolute numbers and as fractions of the observations in the lab.

Tabelle 1. Arten, die im Feld übersehen, später aber bei der Biomasseernte im Labor gefunden wurden. Die Werte sind sowohl als absolute Zahl von Fällen als auch als Anteil der jeweiligen Beobachtungen im Labor angegeben.

Species	# missed in the field	Fraction [%]
Graminoids	29	10
<i>Poa trivialis</i>	7	47
<i>Lolium perenne</i>	3	23
<i>Poa pratensis</i> aggr.	3	43
<i>Arrhenatherum elatius</i>	2	25
<i>Festuca rubra</i> aggr.	2	9
<i>Agrostis capillaris</i>	1	14
<i>Agrostis stolonifera</i>	1	6
<i>Anthoxanthum odoratum</i> aggr.	1	50
<i>Brachypodium pinnatum</i> aggr.	1	25
<i>Bromus sterilis</i>	1	100
<i>Cynosurus cristatus</i>	1	33
<i>Dactylis glomerata</i>	1	8
<i>Elymus caninus</i>	1	100
<i>Festuca pratensis</i>	1	20
<i>Luzula</i> sp.	1	14
<i>Poa alpina</i>	1	14
<i>Poa annua</i>	1	50
Forbs	17	3
<i>Plantago serpentina</i> aggr.	2	33
<i>Ranunculus repens</i>	2	29
<i>Alchemilla vulgaris</i> aggr. s.l.	1	20
<i>Cerastium fontanum</i>	1	14
<i>Daucus carota</i>	1	50
<i>Euphrasia minima</i>	1	33
<i>Fraxinus excelsior</i>	1	50
<i>Lotus corniculatus</i> aggr.	1	8
<i>Plantago lanceolata</i>	1	8
<i>Potentilla crantzii</i>	1	100
<i>Rorippa palustris</i>	1	100
<i>Rumex acetosa</i>	1	13
<i>Rumex alpestris</i>	1	50
<i>Taraxacum</i> sp.	1	9
<i>Trifolium repens</i>	1	8

Table 2. Species that were identified in the field but remained undetected in the lab. The cover estimates are given in the second column. All species except for *Veronica chamaedrys* were missed only once.

Tabelle 2. Arten, die im Feld bestimmt, aber bei der Biomasseernte im Labor nicht wieder gefunden wurden. In der zweiten Spalte ist die Deckungsschätzung im Feld angegeben. Abgesehen von *Veronica chamaedrys* wurde jede Art maximal einmal übersehen.

Species missed in the lab	Cover estimate [%]
<i>Achillea millefolium</i> aggr.	0.7
<i>Cynosurus cristatus</i>	1
<i>Holcus lanatus</i>	1
<i>Leontodon hispidus</i>	0.5
<i>Lolium perenne</i>	0.3
<i>Phleum pratense</i> aggr.	5
<i>Ranunculus acris</i>	0.1
<i>Trollius europaeus</i>	0.5
<i>Veronica chamaedrys</i>	0.2; 0.1

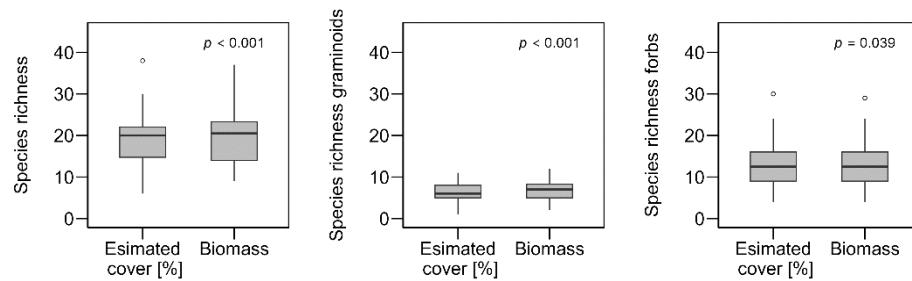


Fig. 3. Comparison of observed species richness in 40 0.09-m² plots based on field sampling with visual cover estimation vs. harvesting biomass and sorting it by species in the lab. The three partial figures from left to right are for all vascular plants, for graminoids alone and for forbs alone, respectively.

Abb. 3. Vergleich des beobachteten Artenreichtums in den 40 0,09 m² grossen Probeflächen zwischen Deckungsschätzung im Feld und Abernten der Biomasse und Sortierung nach Arten im Labor. Die drei Teilaabbildungen zeigen von links nach rechts die Werte für alle Gefäßpflanzen zusammen, für Graminoide und Kräuter separat.

Generally, only species with low to very low fractional biomass were overlooked, with the overlooking probability not exceeding 10% even for the rarest and tiniest plants (Fig. 4). However, graminoids were generally more prone to be overlooked in the field than forbs, with overlooking probabilities up to approx. 20% for species with very low fractional biomass (Fig. 4)

Table 3. Results of the logistic regressions for the overlooking probabilities (OP) of all species, graminoids and forbs dependent on their fractional dry biomass (%BM).

Tabelle 3. Ergebnisse der logistischen Regression für die Übersehenswahrscheinlichkeit (OP) in Abhängigkeit von der anteiligen trockenen Biomasse (%BM) für alle Arten, Graminoide und Kräuter.

Species group	<i>p</i>	Pseudo- <i>R</i> ²	Equation
All	0.004	0.05	$OP = \exp(-2.274 - 0.176 \times \%BM) / (1 + \exp(-2.274 - 0.176 \times \%BM))$
Graminoids	0.005	0.10	$OP = \exp(-1.377 - 0.195 \times \%BM) / (1 + \exp(-1.377 - 0.195 \times \%BM))$
Forbs	0.040	0.07	$OP = \exp(-2.703 - 0.406 \times \%BM) / (1 + \exp(-2.703 - 0.406 \times \%BM))$

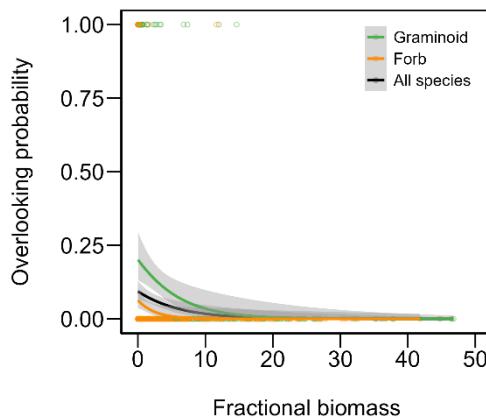


Fig. 4. Probability of having overlooked a species in the field that was subsequently detected in the lab, dependent on the fractional dry mass. The dots represent the observations, while the lines the logistic regressions with their confidence intervals, for all species combined (black), graminoids (green) and forbs (orange).

Abb. 4. Wahrscheinlichkeit eine Art im Feld übersehen zu haben, die nachfolgend im Labor gefunden wurde, in Abhängigkeit von ihrer anteiligen trockenen Biomasse. Die Punkte stehen für die Einzelbeobachtungen, während die Linien die logistischen Regressionen mit ihren Konfidenzintervallen zeigen (schwarz: alle Arten zusammen, grün: Graminoide, orange: Kräuter).

3.3 Translation from biomass to percent cover

The linear mixed model with biomass as a predictor for estimated cover showed the highest conditional R^2 for the version with fractional cover vs. fractional biomass (conditional $R^2 = 0.78$, $p < 0.001$). When this model was run separately for forbs with (conditional $R^2 = 0.79$, $p < 0.001$) and without rosettes (conditional $R^2 = 0.86$, $p < 0.001$), a higher proportion of the variance could be explained. By contrast, the predictive power was worse for graminoids alone (conditional $R^2 = 0.70$, $p < 0.001$) (Fig. 5, Tab. 4).

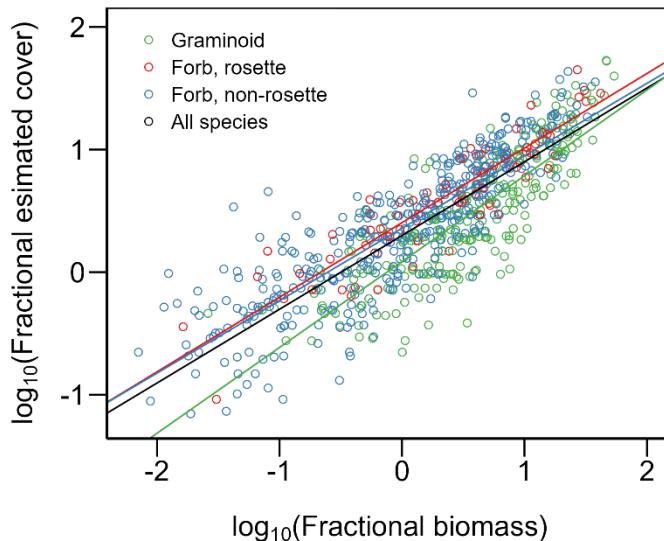


Fig. 5. Relations of the \log_{10} -transformed measured biomass and the \log_{10} transformed estimated cover. The coloured regression lines represent the three growth forms separately, the black line is for all species combined.

Abb. 5. Beziehung zwischen der \log_{10} -transformierten gemessenen Biomasse und der \log_{10} -transformierten Deckungsschätzung. Die farbigen Regressionsgeraden stellen die Regression unterteilt nach Wuchsformen dar, die schwarze Linie für alle Arten.

Table 4. Linear mixed models with measured biomass as a predictor for the estimated cover. Slope and intercept were set random for the different species.

Tabelle 4. Lineare gemischte Modelle mit gemessener Biomasse als unabhängige feste Variable für die geschätzte Deckung und der Artidentität als „random“-Effekt für die Steigung und den Achsenabschnitt.

Regression	Species	Intercept	Slope	Conditional R^2	Marginal R^2	p
Fractional estimated cover [%] ~ Fractional biomass [g]	All	0.30	0.60	0.78	0.71	< 0.001
Fractional estimated cover [%] ~ Biomass [g]	All	0.67	0.56	0.72	0.66	< 0.001
Estimated cover [%] ~ Fractional biomass [g]	All	0.32	0.60	0.75	0.68	< 0.001
Estimated cover [%] ~ Biomass [g]	All	0.71	0.59	0.77	0.71	< 0.001
Fractional estimated cover [%] ~ Fractional biomass [g]	Graminoids	0.09	0.70	0.71	0.69	< 0.001
Fractional estimated cover [%] ~ Fractional biomass [g]	Forbs	0.37	0.60	0.80	0.76	< 0.001
Fractional estimated cover [%] ~ Fractional biomass [g]	Forbs (rosette)	0.40	0.61	0.86	0.82	< 0.001
Fractional estimated cover [%] ~ Fractional biomass [g]	Forbs (non rosette)	0.36	0.59	0.79	0.74	< 0.001

4. Discussion

4.1 Overlooked species

We found on average 0.9 species less with careful cover-based sampling in the field than with biomass sorting in the lab, corresponding to a difference of 4.6% in recorded species richness. One needs to consider that the species list from the field was available in the lab but not the other way round, meaning that in the lab one could specifically search for all species on the list, while this was not possible reciprocally. Had the sampling in the lab been conducted without the species lists from the field, some rare species would likely have been overlooked; thus, the difference in species richness likely would have been slightly smaller. Also, some of the difference might not be due to overlooked specimens, but due to misidentifications. There was also a smaller fraction of cases where species were noted in the field but could not be found in the lab. After carefully checking these cases, we could exclude the possibility that the same species were recorded erroneously under different names.

It is generally accepted in vegetation science that careful sampling can yield relatively complete species lists, but it is impossible to guarantee 100% completeness and correctness with any method, even with the best botanists (Archaux et al. 2009, Klimeš et al. 2001, Lisner & Lepš 2020). In this respect, an overlooking probability of less than 5% is excellent. The values reported by Klimeš et al. (2001) for a species-rich Czech grassland and reviewed from the literature are generally much higher. In Switzerland, Boch et al. (2022) reported 30% overlooked species in dry grasslands and 28% in fens (including wet grasslands) across Switzerland when two observers independently sampled the same 10-m² plots. What could be the cause of the apparently much higher consistency in our case? Possibly, that the plots were two orders of magnitude smaller made it easier to find nearly all species – but see Klimeš et al. (2001), who found that the overlooking probability was higher in smaller plots. Another point might be that the use of direct estimation in percent pushes the observers to search more carefully than the rough 7-step Braun-Blanquet scale did in the case of Boch et al. (2022). Moreover, being aware of the high accuracy of the historic data prompted us to spend more time for sampling in the field than most researchers probably would have done for such small plots.

Not surprisingly, our study found that the probability of being overlooked increased the rarer/tinier a species was and only very rarely occurred for species with a fractional biomass (or cover) above 5% (Fig. 4). Boch et al. (2022) found that the overlooking probability increases monotonously towards the smaller covers, from 3% for 50–75% cover to 52% for cover values below 0.1%, but in their study the fractions of overlooked species were much higher and also reached up to much higher covers.

We found that the growth form has an influence on the likelihood of being overlooked, with graminoids being three times more prone to this than forbs (Table 1). Notorious were *Lolium perenne* and *Poa trivialis*, which often occur together while young individuals of these species can look very similar, thus suggesting that the specimens were taken as one species in the field, while under perfect conditions in the lab they could be distinguished.

4.2 Relationship of cover and biomass

The results of the regression analyses supported the view that there is an allometric relationship between estimated cover and measured aboveground biomass which closely follows a power law (West et al. 1997, Chen & Shiyomi 2019). This indicates that a rela-

tively reliable transformation from biomass to cover or *vice versa* is possible, as previously found in other local or regional studies (Axmanová et al. 2012, Lisner & Lepš 2020, Monzingo et al. 2022). The parameters of our regression functions add to the hitherto limited body of knowledge of such values.

We had expected that the allometric functions would be different for growth forms with strongly different architecture and thus had modelled graminoids, rosette and non-rosette forbs separately. Our results indeed show that one should apply different regression functions for graminoids vs. forbs, while the separation of the two growth forms of forbs had only a negligible effect.

In agreement with the findings of Lisner & Lepš (2020), all our allometric regression functions had exponents of the power law (= slopes in the linearised version of the log-log representation) clearly below 1, in our case between 0.59 and 0.69, in their case between 0.68 and 0.82, meaning that the fractional cover of a species in a plot increases considerably slower than its fractional biomass (this pattern can also be seen in the absolute values). This can easily be explained by the fact that biomass grows in three dimensions, while cover is measured only in two dimensions, leading to an expected value of $2/3 = 0.67$. Interestingly, we found that graminoids had a clearly lower intercept, but higher slope than forbs (Fig. 5). This means that rare graminoids in a plot achieve less cover with a certain dry mass than forbs do, while this difference disappears for the most dominant taxa. For the rarest/tiniest species, the cover/biomass ratio was about three times higher for forbs than for graminoids (Fig. 5: equivalent to a delta of 0.5 on the \log_{10} -transformed y-axis). This pattern is probably mainly due to the narrow upright leaves of graminoids, which cover less in the vertical projection than forb leaves do, since the latter are typically arranged almost horizontally or at least not nearly parallel to the upright stem. Older/bigger individuals of graminoids that have reached their full height then expand laterally by forming dense tussocks or growing stolons/rhizoms.

4.3 Implications for the Square Foot Project

When we started the Square Foot Project (www.zhaw.ch/squarefoot), it was clear that recording the resurvey plots with the method used for the historic plots would not be possible due to cost reasons, especially since each old plot was resurveyed with three to five new plots distributed in the likely area where the historic plot had been located (Riedel et al. 2023). We thus decided for direct estimation in percent, as this method produces much more detailed/reliable data than estimation on an ordinal cover scale, with negligible additional effort (Dengler & Dembicz 2023). This study confirms that this choice was appropriate, since the relationship between importance measures obtained through time-consuming biomass sampling of cut-out sods and the much faster percent estimation in the field is close and can be easily accounted for in statistical models.

That neither the measured biomass data nor the estimated cover values (and the associated richness data) tell the absolute truth is nicely captured by the motto of Lisner & Lepš (2020): *everyone makes mistakes*. To be consistent with the huge majority of vegetation studies (compare the data in sPlot; Bruelheide et al. 2019), we likely will opt to express our results on the cover scale, not on the biomass scale. Regarding species richness, we will have to add 0.9 species (see Fig. 3) to the resurveyed plot to “simulate” what would have been found had we applied the historical method, acknowledging that this is a conservative estimate and the true difference will likely be a bit smaller (see 4.1). Our allometric regressions can be applied for all comparisons that involve species importance (e.g. diversity

indices, species abundance distributions, mean indicator values, community-weighted means/fractions of functional traits). Since for these purposes one usually needs not the absolute cover values, but the fractional importance (p_i), the regressions with fractional values on both axes apply, thus solving the issue that only fractional mass values (and not absolute dry mass values) were available for some of the historical plots. Due to the striking difference between graminoids and forbs, we will have to apply different regressions to these two groups, while a further division of the forbs into subgroups does not appear to be appropriate based on our results. Importantly, despite the high correlation between cover and biomass, the resulting p_i values per species can differ significantly because the exponent of the allometric function is far from 1 – as Chiarucci et al. (1999) has warned. Therefore, the proper solution will be to transform the $p_{i,biomass}$ to $p_{i,cover}$ species by species, then rescale them so that their sum is 1 and only afterwards apply calculation such as biodiversity indices or community-weighted means.

4.4 Conclusions and outlook

We demonstrated that biomass and cover can be converted into each other with a good reliability. While we provide regression functions for Swiss grasslands covering a range of typical grassland species and grassland types found throughout temperate Europe, similar empirical regressions must still be established for other ecosystems. We also noted that even for our unusually small plots of only 0.09 m², the time investment for biomass sampling was four times higher than for careful searching and cover estimation of all species in the field, meaning that the discrepancy will become even bigger for larger plots (as biomass sampling scales linearly with plot size, while the efforts for cover-based plot sampling grows much less). In consequence, we imagine that there will only be a few cases in the future where the enormous additional effort for biomass sampling pays off in terms of more precise data. Even if biomass information is required for certain projects, a cover estimation in percent followed by a transformation based on a pre-study like that at hand might still be preferable. However, this approach only makes sense with cover estimates on a continuous percent scale that resolves the fine differences at the lower end of the scale (particularly below 1%; see Dengler & Dembicz 2023). The same approach can also facilitate the joint use of cover-based and biomass-based importance values in large vegetation-plot databases or the resurvey of other historic plots that have been sampled with a biomass-based approach.

Erweiterte deutsche Zusammenfassung

Einleitung – Die Erstellung von Vegetationsaufnahmen, also die Erfassung aller Arten innerhalb einer definierten Probefläche, ist die am weitesten verbreitete Erhebungsmethode in der Vegetationsökologie. Um die Artmächtigkeit zu ermitteln, werden insbesondere Deckung, Abundanz, Frequenz und Biomasse erhoben. Die Werte können entweder gemessen oder geschätzt werden. Die Deckungsschätzung wird aufgrund des guten Informationsgehaltes, des überschaubaren Zeitaufwandes und der relativ hohen Reproduzierbarkeit am häufigsten angewendet. Die Biomassebestimmung liefert ein noch exakteres Mass der ökologischen Bedeutung einer Art in einer Gesellschaft, ist aber erheblich zeitaufwändiger und zudem destruktiv. In Wiederholungsstudien ist es von Vorteil, die ursprüngliche Methode zu verwenden. Ist dies nicht möglich, so sollte der Zusammenhang der verschiedenen Artmächtigkeits-Methoden bekannt sein, wozu es bisher aber nur wenige Studien gibt. Für die Wiederholungsstudie des Square Foot Projektes (<https://www.zhaw.ch/squarefoot>) lagen für die über 100 Jahre alten Erstaufnahmen nur Biomasseanteile vor. Da wir die pseudo-permanenten Wiederholungsauf-

nahmen mittels prozentualer Deckung erhoben, untersuchten wir exemplarisch den Zusammenhang zwischen den Artmächtigkeits-Methoden Biomasse und Deckung, den Unterschied in der Artenzahl und ob diese beiden Beziehungen von der Wuchsform der Arten abhängig sind.

Methoden – Die 40 Untersuchungsflächen stammen aus Grünlandgesellschaften in der Schweiz zwischen 435 und 2216 m ü.M. (Abb. 1) und unterscheiden sich hinsichtlich ihres Feuchtigkeits- und Nährstoffniveaus. Die Artenvielfalt der 0.09-m² grossen Flächen bei der Felderhebung lag zwischen 6 und 38 Arten mit einem Mittelwert von 18.8 Arten. Für das Abgrenzen und Ausstechen der Grassode wurde ein quadratischer Metallrahmen mit Seitenlänge 30 cm verwendet (Abb. 2). Dieser wurde so positioniert, dass alle im Quadrat wurzelnden Pflanzen eingeschlossen waren. Nach der Deckungsschätzung jeder einzelnen Art in Prozent wurde die Grassode analog der historischen Methode ausgestochen, ins Labor transferiert und dort die oberirdischen Pflanzenteile abgeschnitten, nach Arten sortiert, getrocknet und gewogen. Um die Abweichung zwischen der im Feld und im Labor ermittelten Artenvielfalt zu bestimmen, wurden gepaarte *t*-Tests durchgeführt, für alle Arten, und separat für Graminoide und Kräuter (d.h. alle übrigen Arten). Der Zusammenhang zwischen der Wahrscheinlichkeit, dass eine Art bei der Deckungsschätzung übersehen wird und ihrer Abundanz, wurde anhand einer logistischen Regression bestimmt. Wir wendeten lineare gemischte Modelle mit der Artenidentität als «random»-Effekt an, um Biomasse [g] in Deckung [%] zu übersetzen, sowohl für anteilige wie für absolute Werte von Deckung und Biomasse. Deckung und Biomasse wurden hierfür log₁₀-transformiert. Das beste Modell rechneten wir auch einzeln für die Wuchsformen Graminoide und Kräuter mit und ohne Rosette (die vollständige Artenliste mit Zuteilung der Arten zu den Kategorien sind in Anhang E1 ersichtlich).

Ergebnisse – Der Zeitbedarf für die Feldmethode mit sorgfältiger Suche und Deckungsschätzung lag bei rund 1 Stunde, während die Methode zur Bestimmung des Trockengewichts insgesamt rund 4 Stunden benötigten. Auf den 40 Untersuchungsflächen wurden insgesamt 796 Artbeobachtungen gemacht, wobei 46 Beobachtungen ausschliesslich im Labor und 10 Beobachtungen nur im Feld gemacht wurden (Tab. 1 und 2). Mit der Methode Deckungsschätzung fanden wir im Schnitt 0.9 oder 4.6% weniger Arten auf einer Untersuchungsfläche, als wenn die Individuen abgeschnitten und einzeln sortiert wurden (Abb. 3). Die Übersehenswahrscheinlichkeit war bei Graminoiden dreifach so hoch wie bei Kräutern (Abb. 4). Das Modell, um auf Basis des Trockengewichtes die Deckung vorherzusagen, funktionierte am besten, wenn hierfür jeweils die Anteile verwendet wurden (conditional $R^2 = 0.78$, $p < 0.001$; Tab. 3). Eine Unterteilung der Pflanzen in Kräuter und Graminoide führte zu einer Verbesserung der Vorhersage des Modells, wobei eine weitere Unterteilung der Kräuter in solche mit und ohne Rosette nichts brachte (Abb. 5, Tab. 4).

Diskussion – Mit einer Rate von unter 5% übersehenen Arten im Feld verglichen mit der bestmöglichen Methode (Biomasseernten im Labor), können unsere Felddaten als ungewöhnlich gut gewertet werden. Andere Studien geben in der Regel eine viel höhere Differenz zwischen zwei Methoden oder zwei Forschenden mit der gleichen Methode an (z.B. Boch et al. 2022). Die günstigeren Werte in unserer Untersuchung können auf die kleinere Aufnahmefläche zurückgeführt werden, wobei Klimeš et al. (2001) von einem gegenteiligen Trend berichten.

Die Regressionsanalyse bestätigte, dass eine allometrische Funktion, eine relativ verlässliche Transformation von Biomasse zu Deckungsgrad und umgekehrt ermöglicht. Während Graminoide und Kräuter sich in ihre Funktionsgleichung deutlich unterschieden, war der Unterschied zwischen verschiedenen Wuchsformen von Kräutern vernachlässigbar. Die Exponenten der Potenzfunktion lagen mit 0.59 und 0.69 deutlich unter 1, was sich mit der theoretischen Erwartung und Beobachtungen von Lisner & Lepš (2020) deckt. Dies bedeutet, dass der Deckungsanteil einer Art in einer Untersuchungsfläche langsamer zunimmt als ihr Biomasseanteil. Eine steilere Kurve und ein niedriger Achsenabschnitt bei den Graminoiden (Abb. 5) weisen darauf hin, dass sich diese Wuchsformen deutlich unterscheiden, vor allem bei geringen Deckungen. Hierfür dürften die meist schmalen, aufrechten Blätter der Graminoiden im Vergleich zu den eher horizontal orientierten Kräutern ursächlich sein.

Trockenmasse und Deckung können mit einer hohen Verlässlichkeit ins jeweils andere Mass umgerechnet werden. Die hier vorgestellten Regressionsfunktionen wurden für Grünlandgesellschaften im temperaten Europa ermittelt. Bereits auf einer kleinen Untersuchungsfläche von 0.09 m² war der Zeitbedarf für die Bestimmung des Trockengewichts der einzelnen Arten in etwa vier Mal so hoch wie für eine sehr gründliche Vegetationserhebung mit Deckungsschätzung im Feld. Da die Trockengewichtsbestimmung nur zu einer geringfügig genaueren Aussage führt, müssen Aufwand und Nutzen sorgfältig abgewogen werden. Zur Analyse von Daten mit unterschiedlichen Gewichtungsmassen aus grossen Datenbanken, können allometrische Umrechnungsfunktionen, wie hier präsentiert, eine Lösung bieten.

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Author contributions

The data of this study were collected by O.B. during an internship under the supervision of S.R.. Statistical analyses were carried out by S.W. and S.R., while the manuscript was jointly written by S.R., S.W. and J.D.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1: List of all species found with their assigned growth form and their absolute frequency in the 40 vegetation plots.

Anhang E1: Verzeichnis aller gefundenen Arten mit ihrer Wuchsform und absoluten Häufigkeit in den 40 Vegetationsaufnahmen.

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Supplement E1. List of all species found with their assigned growth form and their absolute frequency in the 40 vegetation plots.

Beilage E1. Verzeichnis aller gefundenen Arten mit ihrer Wuchsform und absoluten Häufigkeit in den 40 Vegetationsaufnahmen.

Species	Family	Growth form	Subform	Frequency	Species	Family	Growth form	Subform	Frequency
Acer pseudoplatanus	Sapindaceae	Forb	non-rosette	1	Hypericum maculatum	Hypericaceae	Forb	non-rosette	1
Acer sp.	Sapindaceae	Forb	non-rosette	1	Hypochaeris radicata	Asteraceae	Forb	non-rosette	1
Achillea millefolium aggr.	Asteraceae	Forb	non-rosette	3	Juncus articulatus aggr.	Juncaceae	Graminoid		1
Acinos alpinus	Lamiaceae	Forb	non-rosette	1	Juncus triglumis	Juncaceae	Graminoid		1
Agrostis alpina	Poaceae	Graminoid		2	Knautia arvensis	Caprifoliaceae	Forb	non-rosette	2
Agrostis capillaris	Poaceae	Graminoid		7	Koeleria pyramidata aggr.	Poaceae	Graminoid		1
Agrostis schraderiana	Poaceae	Graminoid		2	Lathyrus pratensis	Fabaceae	Forb	non-rosette	8
Agrostis stolonifera	Poaceae	Graminoid		18	Leontodon helveticus	Asteraceae	Forb	non-rosette	1
Ajuga reptans	Lamiaceae	Forb	non-rosette	8	Leontodon hispidus	Asteraceae	Forb	rosette	12
Alchemilla fissa aggr.	Rosaceae	Forb	non-rosette	2	Leucanthemopsis alpina	Asteraceae	Forb	non-rosette	1
Alchemilla pentaphyllea	Rosaceae	Forb	non-rosette	1	Leucanthemum vulgare aggr.	Asteraceae	Forb	non-rosette	6
Alchemilla vulgaris aggr.	Rosaceae	Forb	non-rosette	5	Ligusticum mutellina	Apiaceae	Forb	rosette	4
Anemone narcissiflora	Ranunculaceae	Forb	non-rosette	1	Lolium perenne	Poaceae	Graminoid		13
Anemone nemorosa	Ranunculaceae	Forb	non-rosette	1	Lotus corniculatus aggr.	Fabaceae	Forb	non-rosette	13
Anthoxanthum odoratum aggr.	Poaceae	Graminoid		26	Luzula alpina	Juncaceae	Graminoid		1
Anthyllis vulneraria	Fabaceae	Forb	non-rosette	1	Luzula campestris	Juncaceae	Graminoid		1
Arnica montana	Asteraceae	Forb	non-rosette	2	Luzula multiflora aggr.	Juncaceae	Graminoid		4
Arrhenatherum elatius	Poaceae	Graminoid		8	Luzula sp.	Juncaceae	Graminoid		1
Aster bellidiastrium	Asteraceae	Forb	rosette	5	Lycopodium annotinum	Lycopodiaceae	Forb	non-rosette	1
Astragalus australis	Fabaceae	Forb	non-rosette	1	Lysimachia nemorum	Primulaceae	Forb	non-rosette	2
Bartsia alpina	Orobanchaceae	Forb	non-rosette	1	Lysimachia nummularia	Primulaceae	Forb	non-rosette	5
Bellis perennis	Asteraceae	Forb	rosette	2	Mentha aquatica	Lamiaceae	Forb	non-rosette	2
Brachypodium pinnatum aggr.	Poaceae	Graminoid		4	Molinia caerulea	Poaceae	Graminoid		2
Brachypodium sylvaticum	Poaceae	Graminoid		2	Myosotis alpestris	Boraginaceae	Forb	non-rosette	2
Briza media	Poaceae	Graminoid		4	Myosotis sp.	Boraginaceae	Forb	non-rosette	1
Bromus erectus	Poaceae	Graminoid		4	Nardus stricta	Poaceae	Graminoid		9
Bromus sp.	Poaceae	Graminoid		1	Parnassia palustris	Celastraceae	Forb	non-rosette	3
Bromus sterilis	Poaceae	Graminoid		1	Phleum alpinum aggr.	Poaceae	Graminoid		3
Buphtalmum salicifolium	Asteraceae	Forb	non-rosette	1	Phleum hirsutum	Poaceae	Graminoid		1
Calamagrostis epigejos	Poaceae	Graminoid		2	Phleum pratense aggr.	Poaceae	Graminoid		3
Calluna vulgaris	Ericaceae	Forb	non-rosette	1	Phragmites australis	Poaceae	Graminoid		3
Calystegia sepium	Convolvulaceae	Forb	non-rosette	2	Phyteuma orbiculare	Campanulaceae	Forb	non-rosette	3
Campanula barbata	Campanulaceae	Forb	non-rosette	4	Phyteuma spicatum	Campanulaceae	Forb	non-rosette	1
Campanula rapunculus	Campanulaceae	Forb	non-rosette	1	Pimpinella major	Apiaceae	Forb	non-rosette	1
Campanula scheuchzeri	Campanulaceae	Forb	non-rosette	11	Pinguicula alpina	Lentibulariaceae	Forb	rosette	1
Cardamine pratensis aggr.	Brassicaceae	Forb	non-rosette	6	Plantago alpina	Plantaginaceae	Forb	rosette	6
Carex caryophyllea	Cyperaceae	Graminoid		5	Plantago atrata	Plantaginaceae	Forb	rosette	3
Carex echinata	Cyperaceae	Graminoid		1	Plantago lanceolata	Plantaginaceae	Forb	rosette	13
Carex ferruginea	Cyperaceae	Graminoid		3	Plantago major	Plantaginaceae	Forb	rosette	1
Carex flacca	Cyperaceae	Graminoid		2	Plantago media	Plantaginaceae	Forb	rosette	1
Carex flava aggr.	Cyperaceae	Graminoid		1	Poa alpina	Poaceae	Graminoid		7
Carex hirta	Cyperaceae	Graminoid		4	Poa annua	Poaceae	Graminoid		2
Carex montana	Cyperaceae	Graminoid		2	Poa pratensis aggr.	Poaceae	Graminoid		7
Carex nigra	Cyperaceae	Graminoid		4	Poa trivialis	Poaceae	Graminoid		15
Carex pallescens	Cyperaceae	Graminoid		3	Polygonal alpestris	Polygalaceae	Forb	non-rosette	1
Carex panicea	Cyperaceae	Graminoid		3	Polygonal chamaebuxus	Polygalaceae	Forb	non-rosette	2
Carex sempervirens	Cyperaceae	Graminoid		4	Polygonum alpinum	Polygonaceae	Forb	non-rosette	1
Carex sylvatica	Cyperaceae	Graminoid		2	Polygonum bistorta	Polygonaceae	Forb	non-rosette	2
Carex tomentosa	Cyperaceae	Graminoid		1	Polygonum viviparum	Polygonaceae	Forb	non-rosette	5
Carlina acaulis	Asteraceae	Forb	non-rosette	2	Potentilla aurea	Rosaceae	Forb	non-rosette	7
Carum carvi	Apiaceae	Forb	non-rosette	2	Potentilla crantzii	Rosaceae	Forb	non-rosette	1
Centaurea jacea aggr.	Asteraceae	Forb	non-rosette	4	Potentilla erecta	Rosaceae	Forb	non-rosette	9
Centaurea scabiosa	Asteraceae	Forb	non-rosette	1	Potentilla reptans	Rosaceae	Forb	rosette	4
Cerastium cerastoides	Caryophyllaceae	Forb	non-rosette	1	Potentilla sterilis	Rosaceae	Forb	non-rosette	2
Cerastium fontanum	Caryophyllaceae	Forb	non-rosette	8	Primula elatior	Primulaceae	Forb	rosette	3
Cirsium oleraceum	Asteraceae	Forb	non-rosette	1	Primula integrifolia	Primulaceae	Forb	rosette	1
Colchicum autumnale	Colchicaceae	Forb	rosette	2	Prunella vulgaris	Lamiaceae	Forb	non-rosette	9
Convolvulus arvensis	Convolvulaceae	Forb	non-rosette	1	Prunus avium	Rosaceae	Forb	non-rosette	3
Crepis alpestris	Asteraceae	Forb	non-rosette	1	Prunus padus	Rosaceae	Forb	non-rosette	1
Crepis aurea	Asteraceae	Forb	rosette	10	Prunus sp.	Rosaceae	Forb	non-rosette	1
Crepis biennis	Asteraceae	Forb	non-rosette	1	Ranunculus acris	Ranunculaceae	Forb	non-rosette	12
Crepis bocconei	Asteraceae	Forb	non-rosette	1	Ranunculus bulbosus	Ranunculaceae	Forb	non-rosette	2
Crepis capillaris	Asteraceae	Forb	non-rosette	1	Ranunculus ficaria	Ranunculaceae	Forb	non-rosette	1
Crepis paludosa	Asteraceae	Forb	non-rosette	1	Ranunculus montanus aggr.	Ranunculaceae	Forb	non-rosette	7
Crocus albiflorus	Iridaceae	Forb	non-rosette	3	Ranunculus repens	Ranunculaceae	Forb	non-rosette	7
Cynosurus cristatus	Poaceae	Graminoid		3	Ranunculus tuberosus aggr.	Ranunculaceae	Forb	non-rosette	2
Dactylis glomerata	Poaceae	Graminoid		12	Rhinanthus alectorolophus	Orobanchaceae	Forb	non-rosette	5
Dactylorhiza maculata	Orchidaceae	Forb	non-rosette	1	Rhinanthus glacialis	Orobanchaceae	Forb	non-rosette	3
Daucus carota	Apiaceae	Forb	non-rosette	2	Rorippa palustris	Brassicaceae	Forb	non-rosette	1
Deschampsia cespitosa	Poaceae	Graminoid		1	Rubus caesius	Rosaceae	Forb	non-rosette	2
Elymus caninus	Poaceae	Graminoid		1	Rumex acetosa	Polygonaceae	Forb	non-rosette	8
Elymus repens	Poaceae	Graminoid		1	Rumex alpestris	Polygonaceae	Forb	non-rosette	2
Equisetum arvense	Equisetaceae	Forb	non-rosette	2	Salix breviserrata	Salicaceae	Forb	non-rosette	1
Equisetum palustre	Equisetaceae	Forb	non-rosette	2	Salix herbacea	Salicaceae	Forb	non-rosette	1
Equisetum sp.	Equisetaceae	Forb	non-rosette	1	Salix retusa	Salicaceae	Forb	non-rosette	1
Erica carnea	Ericaceae	Forb	non-rosette	1	Salvia pratensis	Lamiaceae	Forb	non-rosette	1
Eriophorum angustifolium	Cyperaceae	Graminoid		1	Sanguisorba minor	Rosaceae	Forb	non-rosette	2
Eriophorum scheuchzeri	Cyperaceae	Graminoid		1	Sanguisorba officinalis	Rosaceae	Forb	non-rosette	3
Eudicotyledonae sp.		Forb	non-rosette	1	Scabiosa lucida	Caprifoliaceae	Forb	non-rosette	2
Euphorbia platyphyllos	Euphorbiaceae	Forb	non-rosette	1	Selaginella selaginoides	Selaginaceae	Forb	non-rosette	4
Euphrasia alpina	Orobanchaceae	Forb	non-rosette	1	Senecio erucifolius	Asteraceae	Forb	non-rosette	1
Euphrasia hirtella	Orobanchaceae	Forb	non-rosette	1	Silene flos-cuculi	Caryophyllaceae	Forb	non-rosette	2
Euphrasia minima	Orobanchaceae	Forb	non-rosette	3	Silene nutans	Caryophyllaceae	Forb	non-rosette	1
Euphrasia rostkoviana aggr.	Orobanchaceae	Forb	non-rosette	1	Soldanella alpina	Primulaceae	Forb	rosette	7
Festuca arundinacea	Poaceae	Graminoid		3	Soldanella pusilla	Primulaceae	Forb	rosette	1
Festuca pratensis	Poaceae	Graminoid		5	Stachys offic				