

Observer and relocation errors matter in resurveys of historical vegetation plots

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Abstract

Aim: Revisits of non-permanent, relocatable plots first surveyed several decades ago offer a direct way to observe vegetation change and form a unique and increasingly used source of information for global change research. Despite the important insights that can be obtained from resurveying these quasi-permanent vegetation plots, their use is prone to both observer and relocation errors. Studying the combined effects of both error types is important since they will play out together in practice and it is yet unknown to what extent observed vegetation changes are influenced by these errors.

Methods: We designed a study that mimicked all steps in a resurvey study and that allowed determination of the magnitude of observer errors only vs the joint observer and relocation errors. Communities of vascular plants growing in the understorey of temperate forests were selected as study system. Ten regions in Europe were covered to explore generality across contexts and 50 observers were involved, which deliberately differed in their experience in making vegetation records.

Results: The mean geographic distance between plots in the observer+relocation error data set was 24 m. The mean relative difference in species richness in the observer error and the observer+relocation data set was 15% and 21%, respectively. The mean “pseudo-turnover” between the five records at a quasi-permanent plot location was on average 0.21 and 0.35 for the observer error and observer+relocation error data sets, respectively. More detailed analyses of the compositional variation showed that the nestedness and turnover components were of equal importance in the observer data set, whereas turnover was much more important than nestedness in the observer+relocation data set. Interestingly, the differences between the observer and the observer+relocation data sets largely disappeared when looking at temporal change: both the changes in species richness and species composition over time were very similar in these data sets.

Conclusions: Our results demonstrate that observer and relocation errors are non-negligible when resurveying quasi-permanent plots. A careful interpretation of the results of resurvey studies is warranted, especially when changes are assessed based on a low number of plots. We conclude by listing measures that should be taken to maximally increase the precision and the strength of the inferences drawn from vegetation resurveys.

KEYWORDS

legacy studies, nestedness, pseudo-turnover, species richness, temperate forest, true turnover, understorey vegetation

1 | INTRODUCTION

The diversity and composition of plant communities have changed dramatically over the last decades (Vellend et al., 2017). Therefore, there is a large interest among scientists, managers and policy makers to document and understand these changes in vegetation over time. Among the methods to study temporal changes in plant diversity, revisits to plots surveyed in the past offer a direct way to observe change

(Chytrý, Tichý, Hennekens, & Schaminée, 2014; Kapfer et al., 2017; Vellend, Brown, Kharouba, Mccune, & Myers-Smith, 2013). Indeed, many vegetation plots have first been recorded multiple decades ago, i.e. in many places before the onset of major environmental changes, and therefore, these legacy data form a unique source of information for global change research (Verheyen et al., 2017). Compiling and maximally exploiting the available historical data on plant communities are therefore an important research priority for vegetation science.



The number of vegetation resurvey studies is steadily increasing, indicating that the scientific community has embraced this challenge (Hédli, Bernhardt-Römermann, Grytnes, Jurasinski, & Ewald, 2017). Recent examples of studies that resurvey legacy data are found across various ecosystems, ranging from mountain tops (Wipf, Stöckli, Herz, & Rixen, 2013), over forests (Naaf & Kolk, 2016), moorlands (Britton, Hester, Hewison, Potts, & Ross, 2017) and hedgerows (Litza & Diekmann, 2017), to prairies (Alstad et al., 2016) and grasslands (Gillet, Mauchamp, Badot, & Mouly, 2016; Stevens et al., 2016). Besides these single region and single system studies, more and more multi-region and/or multi-system studies are emerging (Bernhardt-Römermann et al., 2015; De Frenne et al., 2013). Combining resurveys allows us to check for the generality of community change (Vellend, Baeten et al., 2013) and helps to better understand the relative importance of, and interactions between, the different drivers of change (Verheyen et al., 2017). These combined resurvey studies can complement community monitoring networks, such as National Forest Inventory programmes or country-level surveys, which generally cover shorter time periods, but have more solid designs ensuring representativeness and statistical robustness.

Despite the important insights that can be obtained from resurveying historical vegetation plots, the approach is prone to several types of error (Kapfer et al., 2017). Two important error types are observer and relocation errors. The first type of error, observer error, arises because the initial surveys and recent resurveys are typically done by different surveyors and, when comparing across resurvey data sets of multiple regions, surveyors usually also differ. This type of uncertainty has been well studied (Archaux, 2009; Kirby et al. 1986; Lepš & Hadincová, 1992; Vittoz & Guisan, 2007). In a recent review, Morrison (2016) found that the percentage of species detected by one observer but not by others (a phenomenon coined "pseudo-turnover" by Nilsson & Nilsson, 1985) is typically anywhere between 10% and 30%. Burg, Rixen, Stöckli, and Wipf (2015) benchmarked pseudo-turnover due to observer error against turnover over time on Alpine mountain summits and found that the observer-related pseudo-turnover was almost three times smaller than the actual changes observed over one century (13.6% and 41.4%, respectively), confirming the presence of true floristic changes over time.

Relocation errors, on the other hand, are caused by the imperfect relocation of the historical plots in the field. The majority of resurvey studies, and especially those working with plots first established many decades ago, work with so-called quasi-permanent plots (*sensu* Kapfer et al., 2017; also referred to as semi-permanent plots). Quasi-permanent plots are plots that were never permanently marked in the field (e.g. by means of paint markings on trees or metal poles inserted in the soil). Hence, only the approximate plot location is known, e.g. via descriptions, sketch maps or markings on topographic maps. Relatively few studies have attempted to quantify the inaccuracies introduced by imperfect relocation (Fischer & Stöcklin, 1997; Kopecký & Macek, 2015; Ross, Woodin, Hester, Thompson, & Birks, 2010). Kopecký and Macek (2015) compared long-term vegetation changes in permanent vs quasi-permanent plots in the same

region of the Czech Republic. They found similar temporal changes in multivariate plot composition in both plot types and concluded that resurveys are apparently robust against relocation errors. Fischer and Stöcklin (1997) and Ross et al. (2010) came to a similar conclusion by comparing the present-day spatial turnover in the vegetation composition with the turnover over time. They assessed the spatial turnover by recording multiple vegetation plots at varying distances from the likely location of the historical vegetation plot.

Here, we quantify the contribution of observer and relocation errors in resurvey studies across multiple regions in Europe. As outlined above, observing temporal changes in the vegetation seems to be robust against the individual types of error, but it is unknown whether this conclusion still holds when both types of uncertainty are combined and when looking across multiple resurvey data sets. This is of crucial importance, because in most resurvey projects both errors will play out together. Therefore, we designed a study that mimicked all steps in a typical resurvey study and that allowed determination of the magnitude of observer errors only vs joint observer and relocation errors. Vascular plants growing in the understorey of temperate forests were selected as the focal community, given the rapidly growing number of resurvey studies that have been performed in this system over the past few years (see Verheyen et al., 2017). The study covered ten regions across Europe to explore generality across contexts (e.g. quality historical data, forest types) and involved no less than 50 observers, which deliberately differed in their experience in making vegetation records (from students to experienced botanists). The latter is important since the level of training is known to vary strongly between resurvey projects and can have an important impact on the (re)survey outcome (Seidling et al., 2014). The following research aims were addressed: (a) quantify the differences in geographic location, species richness and species composition between the records made by different surveyors in independently relocated plots (observer+relocation error) and compare with differences due to observer error only (not for geographic location); (b) determine the degree to which the between-record variation in geographic location, species richness and species composition can be explained by surveyor experience; and (c) explore the impact of the observer and relocation error on inferences about the changes in species richness and community composition over time.

2 | METHODS

2.1 | Study design and data collection

To closely mimic the procedure that is usually adopted when performing resurveys of quasi-permanent plots, we undertook the following steps: identify suitable legacy data, select plots, gather a team of surveyors and perform the field measurements. First, suitable data sets were selected that met the following criteria:

- Plots are located in a single forest or landscape in the temperate

forest zone in Europe (further referred to as a region);

- Given the interest in documenting long-term vegetation changes, the plots were first surveyed at least two decades ago;
- The first survey was done by an experienced botanist to minimize the chances of species being overlooked and misidentification in the historical data;
- The original survey methods (e.g. survey date, plot shape and size, definition of vegetation layers, nomenclature) are well documented;
- The plots are quasi-permanent, i.e. they have not been permanently marked so that relocation relies on field notes, maps and/or canopy descriptions.

We selected ten legacy data sets from different regions throughout Europe, covering a range of forest types and contexts (Table 1). The dates of the first surveys ranged from 1930 to 1936 up to 1995 and plot sizes varied between 25 m² and 400–600 m².

In the second step, five plots were randomly picked from each of the selected data sets, provided that no major disturbances, such as canopy removal or soil disturbance, had taken place in the plot locations since the time of the first sampling. This criterion allows benchmarking of our error estimations with minimum vegetation change scenarios: if the obtained error estimates are significantly smaller than the observed temporal vegetation changes in the absence of a major disturbance, then we are confident that we will pick up real changes in more disturbed conditions as well.

Third, a team of five surveyors with different levels of vegetation survey experience was formed in each of the ten regions. We distinguished three levels: junior surveyors have surveyed less than 100 plots throughout their career, intermediates have surveyed between 100 and 500 plots, and seniors have surveyed more than 500 plots. Each region had at least one person per experience category in its team. In total 20 senior, 17 intermediate and 13 junior surveyors were involved. As expected, the level of experience and the age of the surveyors were positively correlated ($r_{\text{Spearman}} = 0.48$ with $p < 0.001$ and $n = 50$).

In the fourth step, each team performed the resurvey. The actual field campaign consisted of three stages (see Figure 1 for a schematic representation):

- *Plot location* – Using the available historical information (Table 1: “Location info”), each team member individually relocated the most likely plot centre. To do so, the team travelled together to an unequivocal landmark (e.g. a crossroad or a bridge over a small stream) and from there one team member after the other went into the forest to search for the most probable location of the plot centre. This location was discretely marked. With all five team members relocating a historical record, this resulted in five “plot realizations” of the same quasi-permanent plot. Finally, all team members returned to the location they marked and the pair-wise geographic distances between all the centres of the five plot realizations were measured.

- *Observer+relocation error* – The team members then established a plot at “their” location and made a vegetation survey, by recording the presence of all vascular understorey plant species. The definition of “understorey” varied somewhat between regions because the definition of the original survey was used. In most cases, the understorey was defined as all vascular plants – woody and non-woody – below 1.5 m in height.
- *Observer error* – Finally, one of the five plot realizations was randomly picked and the four other team members repeated the vegetation description for that location. These records thus differ only because of observer error.

This protocol ultimately resulted in two data sets: an observer+relocation error data set covering ten regions, and an observer error data set covering nine regions (the French team did not perform the observer error only surveys). Note that the observer error may involve several types of uncertainty. In our field protocol, all species’ identifications were double-checked by the senior surveyor(s) and no cover estimates were performed. This means we opted to focus on overlooking error only, and not on misidentification nor (cover) estimation errors (sensu Morrison, 2016), since overlooking errors is considered to be the most important source of error (Archaux, 2009). All resurveys were performed in spring or summer 2016, based on the period of the initial survey.

2.2 | Data analysis

To address our first research aim (a), we quantified the differences in geographic location, species richness and species composition between the vegetation records of each quasi-permanent plot. For the observer+relocation error data set, this means we looked at the variation between the five records made by the different surveyor at “their” plot location (i.e. alternative plot realizations). For the observer error data set, we quantified the variation between the records of the different surveyors recording the same plot location; the difference in geographic location was thus zero. We used pair-wise metrics to quantify the differences among all ten possible combinations of the five records within each quasi-permanent plot. *Geographic location*: we simply used the pair-wise distances (in metres) between the records that were measured in the field (only relevant for the observer+relocation error data set). *Species richness*: we worked with a relative difference in species richness $|S_i - S_j| / \max(S_i, S_j)$, with S_i and S_j the number of species in records i and j , respectively ($i \neq j$). *Species composition*: we used a pair-wise dissimilarity metric $(S_i + S_j - 2J) / (S_i + S_j)$, with J the number of species that occur in both compared records. This dissimilarity is known as the Sørensen dissimilarity and has been generally used in studies on observer error to quantify what is commonly called “pseudo-turnover” (Morrison, 2016). We note that the term “turnover” is misleading here, because this metric also quantifies nestedness patterns derived from richness differences, in addition to pure turnover (Baselga, 2010). After calculating the pair-wise differences among records (richness, composition and the natural logarithm of

TABLE 1 Overview of the study regions (ranked alphabetically), the plot characteristics and the composition of the survey teams

Region (N, E)	Country	Forest type ^a	Year first survey	Plot size (m ²)	Location info ^b	Resurvey team ^c
Białowieża (52°44', 23°52')	PL	FAG-03 <i>Carpinetalia betuli</i> P. Fukarek 1968	1949	100	M/D/C	S (52)/S (28)/I (49)/J (38)/J (34)
Brandenburg (52°34', 13°00')	DE	FAG-03 <i>Carpinetalia betuli</i> P. Fukarek 1968	1964–1970	400	M/C	S (56)/S (52)/I (37)/I (33)/J (23)
Czech Karst (49°54', 14°07')	CZ	FAG-03 <i>Carpinetalia betuli</i> P. Fukarek 1968	1974	400	M/D/C	S (40)/S (34)/I (32)/I (30)/J (29)
Flemish Ardennes (50°55', 3°43')	BE	POP-02 <i>Alno-Fraxinetalia excelsioris</i> Passarge 1968	1980	100–200	M/C	S (47)/I (42)/I (33)/J (32)/J (28)
Nyírség (47°46', 22°16')	HU	POP-02 <i>Alno-Fraxinetalia excelsioris</i> Passarge 1968	1930–1936	25	M/D/C	S (55)/S (28)/I (58)/I (28)/J (29)
Pálava (48°53', 16°39')	CZ	FAG-03 <i>Carpinetalia betuli</i> P. Fukarek 1968	1953–1963	400–600	M/D/C	S (39)/S (31)/I (44)/I (30)/J (22)
Poľana Mts. (48°37', 19°21')	SK	FAG-03 <i>Carpinetalia betuli</i> P. Fukarek 1968	1964	500	M/D/C	S (47)/S (41)/I (36)/J (36)/J (29)
Sogn og Fjordane (61°46', 5°56')	NO	FAG-05 <i>Aceretalia pseudoplatani</i> Moor 1976	1979–1980	25	D/C	S (55)/S (48)/I (36)/I (34)/J (38)
Sudetes (51°01', 6°44')	PL	PUB-01 <i>Quercetalia pubescenti-petraeae</i> Klika 1933	1990–1992	200	M/C	S (50)/S (45)/S (33)/I (29)/J (28)
Thiérache ^d (49°45', 3°57')	FR	FAG-03 <i>Carpinetalia betuli</i> P. Fukarek 1968	1995	200–500	M/C	S (45)/S (28)/I (39)/I (34)/J (34)

^aOrder-level classification according to Mucina et al. (2016). ^bAvailable information to relocate the plot; M: Map; D: Written descriptions; C: Canopy data recorded at the time of the first survey. ^cS: Senior; I: Intermediate; J: Junior. Surveyor age in 2016 is indicated between brackets. ^dThe observer error only data set is not available for this region.

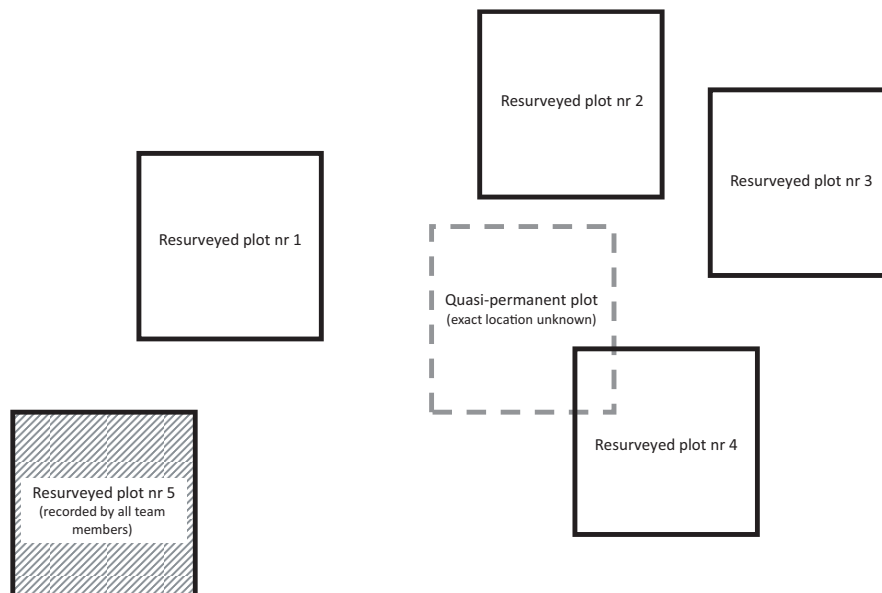


FIGURE 1 Schematic representation of the sampling procedure. The quasi-permanent plot (with unknown exact location) was relocated and resurveyed by each of the five survey team members in the best possible way (plot “realizations” no. 1 – 5). These records involve observer+relocation error. Then, one of the five plot realizations was randomly selected and the four other team members repeated the vegetation description for that plot (nr 5 in this example) to determine the observer error only

geographic distance), their variation was modelled with multilevel models of the form $y_i = \mu + \text{region}_{j[i]} + \text{plot}_{k[i]} + \varepsilon_i$ (model 1). Here μ was the grand mean for the between-record differences in richness, composition and geographic distance within quasi-permanent

plots. The group-level effects region ($j = 1, \dots, 10$) and quasi-permanent plot ($k = 1, \dots, 50$) accounted for the clustering of records within these groups and were assumed to come from separate independent zero-mean normal distributions, e.g. $\text{plot}_k \sim N(0, \sigma_{\text{plot}}^2)$. The

residual errors were assumed to be drawn from $\epsilon_i \sim N(0, \sigma^2)$. Models were fitted with the probabilistic programming language Stan, from R v 3.4.0 through the *brms* package (Bürkner, 2017; R Foundation for Statistical Computing, Vienna, Austria). We used the default priors for these multilevel models, i.e. a zero-mean normal distribution with SD of 1 or, for the variance parameters, a Student *t* distribution with $\sigma = 10$ and 3 *df*. We ran four chains of a thousand iterations each, after a warm-up of one thousand iterations.

A recent review study on observer error (Morrison, 2016) listed the mean Sørensen dissimilarities (\pm SD) reported in 17 published studies across different vegetation types. We took the opportunity to directly compare the compositional differences in the present study to the results reported in those previous studies. Therefore, we performed a formal meta-analysis on the Morrison data, using a multilevel meta-analytic model $z_j = \mu + u_j + m_j$ (model 2; “random effects” meta-analysis). Here z_j was the mean dissimilarity for the *j*th study ($j = 1, \dots, 17$), μ the meta-analytic mean, u_j the study-specific effect that was normally distributed around zero with between-study variance σ_u^2 and m_j the sampling error effect for each study, which is also normally distributed around zero with the corresponding sampling error variance σ_m^2 reported in the review (Nakagawa & Santos, 2012). The model was fitted again with Stan, using the same settings as above.

Our second aim (b) was to determine whether the between-record variation in geographic location, species richness and species composition was explained by surveyor experience (junior, intermediate, senior). The same base model of the first analysis was used (model 1), but the grand mean μ was replaced by another linear predictor. *Geographic location*: for the pair-wise geographic distance between records, we replaced the grand mean with a predictor “surveyor combination”. The six levels of this predictor were defined by the experience of the surveyors that made the compared records, e.g. “junior – intermediate” for a distance between records made by a junior and intermediate surveyor. *Species richness*: the number of species in a record was modelled with an intercept for each of the three surveyor experience levels. Since plot sizes differed somewhat between regions, we also added a slope for the plot size, which was normalized to average of zero, so that intercepts were fitted for average-sized plots. Plot size was not log-transformed here, because richness increased in rather a linear way with size (plot sizes were relatively small and probably in the first part of a species–area curve; Supporting information Appendix S1). Besides the group-level effects for region and plot, we added an additional effect for surveyor identity to account for the multiple records made by the same person. *Species composition*: we first decomposed each pair-wise Sørensen dissimilarity (cf. first analysis) into its two additive components: a pure turnover term and a term quantifying nestedness due to richness differences (Baselga, 2010). Then, the pair-wise dissimilarities (turnover, nestedness) between the records were modelled by the predictor “surveyor combination” (see analysis geographic location). For the observer+relocation error data set, the geographic distance between the records was added as a predictor, because

records made in plot realizations that were further apart may involve larger compositional differences. The models were fitted again with Stan, using the same settings as above.

The third aim (c) was to explore how the observer and relocation errors may influence the inferences about temporal changes in species richness and community composition. Here, we used the same approach as in the first analysis but making pair-wise comparisons of records over time instead of across space. First, for each quasi-permanent plot, we calculated the pair-wise relative difference in species richness and the Sørensen dissimilarity between the vegetation record of the initial survey (legacy data set) and each of the five resurveys of the present study. The pair-wise differences were modelled with model 1 again, first on the entire data set and then on the subsets of data including junior-only or senior-only data. These subsets allow exploration of how surveyor experience influences inferences about the temporal changes in vegetation.

3 | RESULTS

The mean geographic distance between plots in the observer+relocation error data set was 24 m (95% CI = [15.3–36.0]) (Figure 2). Differences between regions were significant, ranging from a mean distance of 10 m in the Flemish Ardennes (BE) up to 45 m in the Pol'ana Mountains area (SK; Supporting information Appendix S2).

The mean relative difference in species richness in the observer error data set was 15% (Figure 2; Supporting information Appendix S2). With a mean species richness estimate for an average-sized plot (ca. 260 m²) of 36 species, a 15% difference corresponds to the recording of ± 6 species. The mean relative difference in species richness in the observer+relocation data set was higher (21%), although the 95% credible interval overlapped with the observer error-only interval. The mean difference in species composition between the five records at a quasi-permanent plot location (Sørensen dissimilarity) was on average 0.21 and 0.35 for the observer error and observer+relocation error data sets, respectively (Figure 2; Supporting information Appendix S2). The relocation error clearly leads to additional compositional variation between records compared to the observer error only. Interestingly, the mean dissimilarity found in our observer error only data set corresponded very well to a meta-analytic mean dissimilarity of 0.18 reported in the recent literature (Figure 2).

More detailed analyses of the geographic distance between the plot locations in the observer+relocation error data set showed no effect of surveyor experience (Figure 3). The between-record variation in species richness, however, showed that juniors found significantly less species compared with seniors and intermediates when only observer error was involved; surveyors with intermediate or senior experience did not differ here. When both observer and relocation error were involved, less experienced surveyors (junior and intermediate) found significantly lower richness values compared with more experienced colleagues (second column Figure 3). Compositional

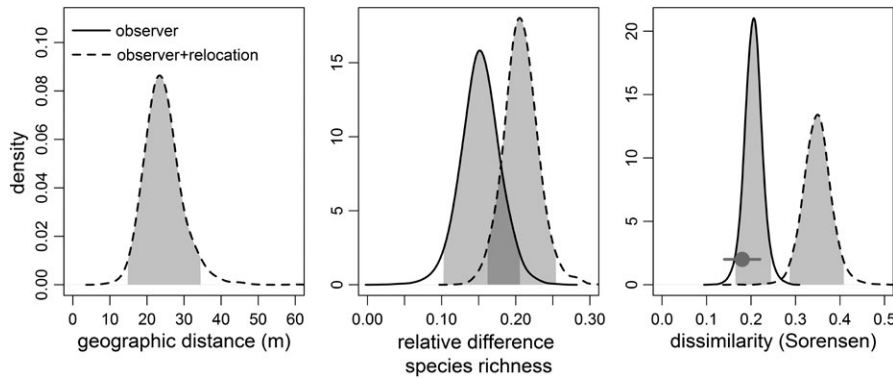


FIGURE 2 Mean pair-wise differences in geographic location (left), species richness (mid) and species composition (right) between the vegetation records within quasi-permanent plots. Two data sets were analysed separately: one involving observer error only (different surveyors sampling the same plot location) and one involving both observer and relocation error (different surveyors sampling an individually relocated plot). Results show the posterior distribution of the mean of the pair-wise differences within quasi-permanent plots, with the 95% highest posterior density intervals shaded in grey. The geographic distance is simply the distance in meters between the locations of the records and is only relevant for the observer+relocation error data set. The relative difference in species richness between records was scaled by the maximum richness of the records. The compositional difference was calculated as a pair-wise Sørensen dissimilarity. The right panel also shows the result of a meta-analysis on the compositional dissimilarity across 17 published observer error studies (Morrison, 2016): meta-analytic mean compositional dissimilarity across observers with 95% intervals as grey horizontal error bars

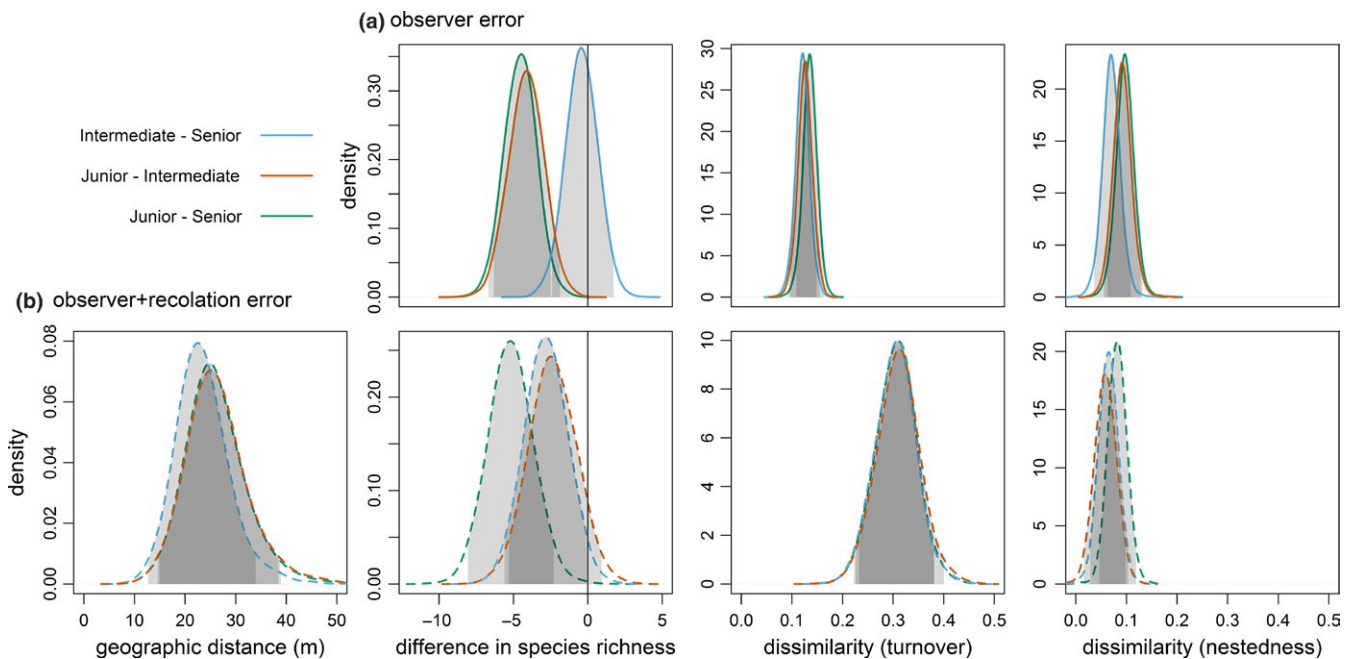


FIGURE 3 Mean pair-wise differences in geographic location, species richness and species composition between the vegetation records of surveyors with different levels of experience. Two data sets were analysed separately: observer error (top row) and observer+relocation error (bottom row). Differences between three surveyor combinations are shown, excluding comparisons within a level of experience (e.g. mean difference in richness between the records of two junior surveyors). Results show the posterior distribution of the mean of the pair-wise differences within quasi-permanent plots, with the 95% highest posterior density intervals shaded in grey. Geographic distance is the distance in meters between the locations of the records and is only relevant for the observer+relocation error data set. The mean difference in species richness is given for an average-sized plot and was calculated so that negative values imply higher species richness in the records made by the more experienced surveyor (e.g. junior-senior). Two components of compositional dissimilarity are shown: replacements of some species by others (turnover) and richness differences between surveyors creating nestedness patterns across their records (nestedness)

variation between records was largely due to some species replacing others across the records (turnover > nestedness component), so a surveyor who found species that others did not find and *vice versa*.

This was especially true for the observer+relocation error data set, with clearly higher turnover values compared with the observer error only data set (third column Figure 3). Surveyor type did not,

however, explain the turnover degree between records. The degree to which records showed nestedness patterns (last column Figure 3) was somewhat related to observer type, consistent with the differences in species richness. The largest values were found for records made by juniors vs seniors or intermediates, partly because juniors simply missed a number of species creating nestedness patterns across the records. The mean dissimilarity due to nestedness was comparable between the two data sets. The geographic distance between the plot locations did not explain compositional dissimilarity (turnover and nestedness) in the observer+relocation error data set. Together, results on the compositional variation showed that the nestedness and turnover components were of equal importance in the observer data set, whereas turnover was much more important than nestedness in the observer+relocation data set.

Interestingly, the differences between the observer and the observer+relocation data sets largely disappeared when looking at temporal change: both the changes in species richness and species composition over time were very similar in these data sets (Figure 4). The mean change in species richness across regions was centred around zero, but in some regions the trend for junior surveyors deviated from the general trend. As junior surveyors tended to find less species (Figure 3), they found a smaller mean increase in species richness in regions where richness tended to increase over time, and a larger mean decrease in richness in regions with overall decreasing richness (Figure 4 top row). The mean temporal change in composition in both data sets was high: 0.51 (95% CI = [0.44–0.59]; observer error) and 0.50 (95% CI = [0.43–0.57]; observer+relocation error). In two regions ((Sogn og Fjordane (NO) and Nyírség (HU)), the compositional change over time was clearly higher for the plots recorded by the junior surveyors, especially in the observer+relocation data set.

4 | DISCUSSION

We were able to quantify and disentangle the observer and relocation errors when resurveying quasi-permanent vegetation plots. A large number of observers were involved in the present study, covering ten temperate forest regions, with different plot sizes, initial survey dates and original plot descriptions. Hence, our results likely represent the range of errors that can be encountered in these systems. Below, we discuss the main findings using our research questions as the backbone. We conclude with recommendations for future resurvey studies.

4.1 | Quasi-permanent plots cannot be perfectly relocated

Our results demonstrate that surveyors hardly ever located the plots to be resurveyed on the same spot (pair-wise distance <5 m in only 8% of the cases); generally, distances spanned up to several tens of meters. Kopecký and Macek (2015) reported a mean distance of 27 m between database stored coordinates and tree markings of permanent plots in the Czech Republic. This is in line with the mean

pair-wise plot distance of 24 m observed in our study. The large variation in pair-wise distances among relocated plots between the ten study regions (Supporting information Appendix S2) was most likely due to differences in forest characteristics and the quality of the descriptions of the historical plots. Relocation is, for instance, more difficult in large forests with a low density of unequivocally retrievable landmarks such as crossroads, bridges, etc., and in forests with little variability in topography and canopy composition. Ambiguous and imprecise descriptions of the original plot location will obviously render the plot relocation more difficult. Given the importance of the relocation error we found here, resurvey projects should preferably be initiated only when high quality historical information is available.

4.2 | Observer and relocation errors lead to significant errors in the estimation of species richness and composition

The differences in richness estimates (15%) between observers were very comparable to the 19.2% reported by Archaux (2009). The larger figure from Archaux could be because this survey also included bryophytes, which are generally more easily overlooked. We should stress, however, that our protocol only focused on overlooking errors and eliminated identification errors as much as possible. Although the latter error is deemed to be relatively small (e.g. 5.3% at the species level according to Archaux, 2009), our error estimates have to be interpreted as minimum errors that can be encountered. The estimated observer error only on composition (21%) was also very similar to the mean compositional variation reported in the literature (Morrison, 2016). The imperfect relocation of the plots added additional variability to the richness and, especially, composition assessments, with error estimates of 21% and 35%, respectively. This is not surprising as the relocated plots were often several tens of meters apart (Figure 2; Supporting information Appendix S2). Indeed, it has been shown that large compositional changes can occur at this scale. For instance, Vanhellemont, Baeten, and Verheyen (2014) reported mean herb layer dissimilarity values of *ca.* 0.8 between 10 m × 10 m plots laid out in two 1-ha zones in two contrasting forest types in Belgium. In their study, the nestedness and turnover components accounted for 0.2 and 0.6 of the dissimilarity, respectively. Hence, inferences about temporal changes in species richness and composition in individual plots should be interpreted with care as differences less than *ca.* 25% and *ca.* 40%, respectively, could simply result from observer and relocation errors (cf. Morrison, 2016). Directional changes in community properties, such as changes in species richness, could still be detected when a sufficiently large number of plots are combined. The 21% error on species richness estimates would mean that at least ~25 survey–resurvey plot pairs are needed to detect a 20% difference in species richness at $\alpha = 0.05$ and with a power of 0.90 (Neter, Wasserman, & Kutner, 1990: 1152). The high degree of uncertainty associated with estimates of (changes in) species richness probably helps to explain why meta-analyses of temporal

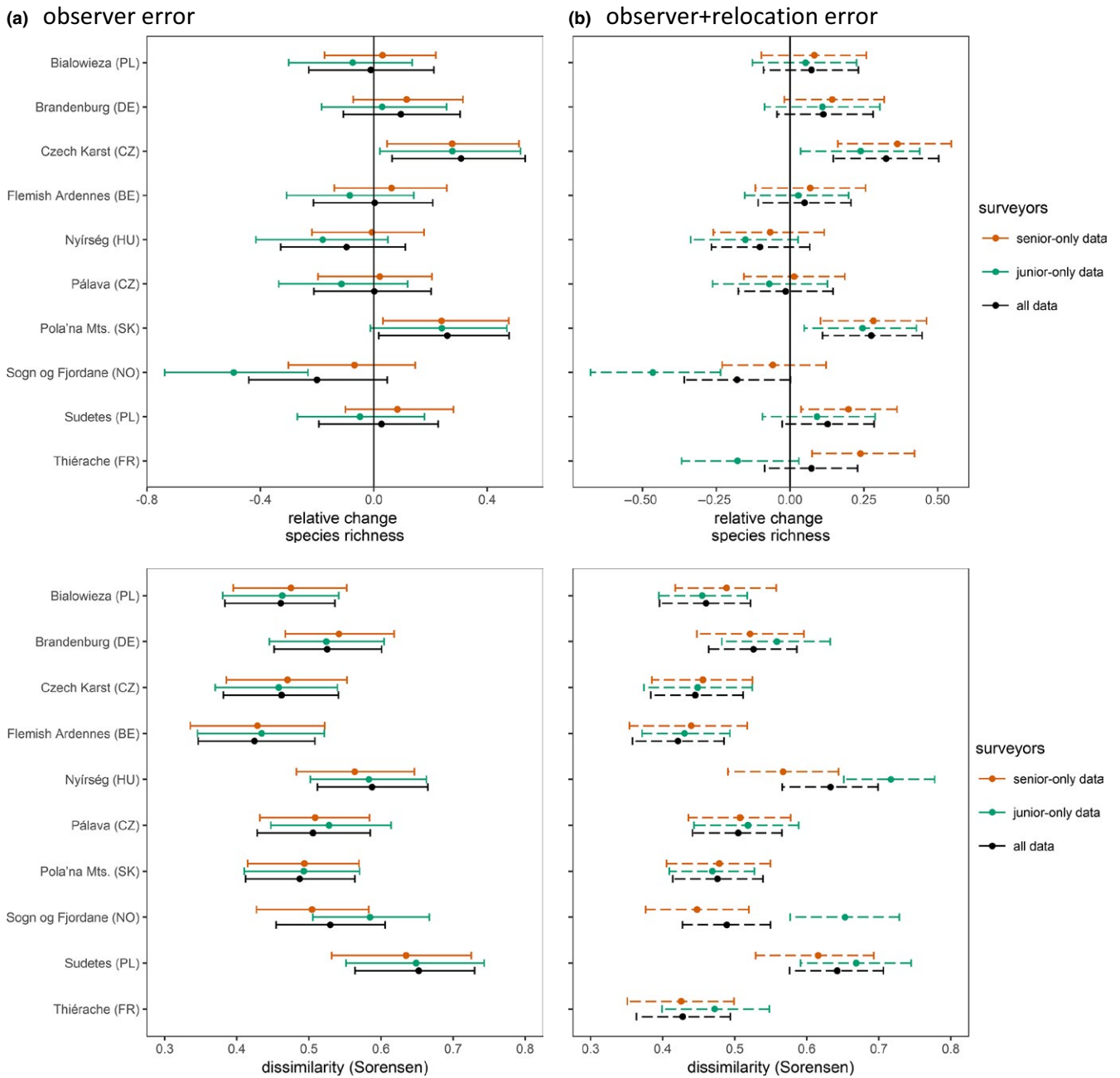


FIGURE 4 Mean temporal change in species richness (top row) and species composition (bottom row) in ten European regions. In each region, five quasi-permanent plots were selected from a legacy data set and resurveyed by five different observers recording either one relocated plot location (observer error; left column) or five individually relocated plot locations (observer+relocation error; right column; see Figure 1). Results show the mean change and 95% credible interval in richness or composition within quasi-permanent plots over time. The relative difference in species richness between the initial vegetation record (legacy data set) and a re-recording of the same quasi-permanent plot (current study) was scaled by the maximum richness of the two records, while the change in composition is expressed as a pair-wise Sørensen dissimilarity. In each region, resurveys were made by five different surveyors and the graphs show the result using the data from all surveyors, or the subsets of data including only the senior or the junior surveyors. The regions are ranked alphabetically

changes in vegetation richness and diversity often do not find a net change over time (Bernhardt-Römermann et al., 2015; Vellend, Baeten et al., 2013; Verheyen et al., 2012). (Dis-)similarity-based metrics of community composition change are non-directional, and increasing the number of plots will not help to increase the signal-to-noise ratio. Hence, other approaches may be needed, as discussed below.

4.3 | The expertise of the surveyor matters

In line with the majority of earlier studies (for an overview, see Morrison, 2016), we observed an underperformance of surveyors with little experience, expressed as the number of vegetation plots recorded in their career. Junior surveyors found on average five species less than more experienced researchers (Figure 2), which was

also reflected in the nestedness of their records within the more species-rich records of the other surveyors. The vegetation turnover component in the observer error only data set was, however, of the same order of magnitude as the nestedness component, indicating that to some extent also different species are seen by the observers. Interestingly, surveyor experience did not help to explain variation in the turnover component in the observer+relocation data set, confirming that the dissimilarity between the plots in this data set is to a large extent caused by the spatial turnover in composition present in the vegetation. Based on our experience with resurvey studies in forests (Verheyen et al., 2017), it became clear that resurvey projects are often performed by unexperienced researchers, such as MSc students. The results presented here clearly show that supervisors of such projects should pay a lot more attention to good training. This would avoid elevated estimation errors and even biased outcomes, as suggested by the analysis of temporal changes in species richness depicted in the top row of Figure 4. Involving more experienced surveyors and using multiple observers per plot have been recommended as strategies to reduce the observer error (e.g. Archaux, 2009; Morrison, 2016). However, note that the spatial turnover in composition due to relocation error, which is responsible for a large part of the dissimilarity between records, will not be affected by these measures.

4.4 | Interpreting temporal changes in richness and composition should be done with care

The similar temporal changes in richness and composition in the observer error only and the observer+relocation error data sets are not surprising when considering that both data sets actually involve relocation error when comparing to an old vegetation plot. Indeed, looking across time, the location of the plot used for the observer error only is not necessarily closer to the exact location of the historical record. The results depicted in Figure 4 allowed us to confirm temporal changes in richness in only two out of ten regions, which is at least partly due to the errors associated with richness estimates and the too low number of plots used, as discussed above. In contrast, true compositional changes over time were more common, with an overall mean compositional dissimilarity of ca. 50% (i.e. well above the 40% threshold value mentioned above). The latter is in line with Burg et al. (2015) who found three times higher compositional dissimilarity over time than between observers and concluded that temporal changes reflected a true ecological pattern. Large changes in composition exceeding 40% are indeed often observed (Verheyen et al. (2012, for a synthesis of 23 resurvey data sets of temperate forest understorey vegetation), meaning that true compositional changes will have occurred in most resurveys studies. However, the unknown accuracy of resurveys and the low precision of the obtained estimates of taxon-based compound community descriptors argue for a different approach to analysing resurvey data. Lumping data in metrics such as species richness and community (dis)similarity removes all species-level information and masks important directional changes in individual species or species groups. Recent

quantitative developments such as model-based approaches in community ecology now allow quantifying changes in community composition directly from the data that were observed, i.e. the changes in species presences or abundances (Ovaskainen et al., 2017; Warton et al., 2015). Specifically in the context of resurvey studies, we recently developed an approach that looks for species-level effects of time period to construct a multiple-site metric that quantifies the degree to which individual species responses are consistent and result in directional changes in community composition (Baeten et al., 2014). The unknown accuracy and low precision of the taxon-based methods also call for more mechanistic, hypothesis-driven research in this field. A priori identifying the potential drivers of change in combination with Ellenberg indicator values (Diekmann, 2003) and/or a trait-based approach, e.g. via the response-and-effect framework (Suding et al., 2008), to translate driver impacts into expected patterns of functional composition changes will enable robust quantification of directional changes over time. Recent examples of such species-oriented and trait-based approaches are Ash, Givnish, and Waller (2017) and Li and Waller (2017), respectively.

5 | CONCLUSIONS

Our results demonstrate that observer and relocation errors are non-negligible when resurveying quasi-permanent plots. A careful interpretation of the results of resurvey studies is warranted, especially when changes in richness are assessed based on a low number of plots (e.g. less than several dozen). Whereas the low precision of the obtained estimates of community change is to some extent unavoidable in this type of study, we argue that the following measures should be taken to maximally increase the precision and strength of the inferences that can be drawn:

- Only perform a resurvey study when the quality of the original plot descriptions is sufficiently high to relocate and resurvey the plots;
- Perform resurvey studies with well-trained surveyors or with teams of surveyors to minimize the observer error;
- Quantify and report the observer and the relocation error in every study by applying the protocol proposed here in a subset of the resurveyed plots;
- Significant directional changes in community properties, such as species richness, will only surface when several dozen plots can be resurveyed, given the high error associated with the estimation of these properties;
- Consider alternatives to compound (dis-)similarity-based descriptions of community change, such as methods that quantify changes in individual species and hypothesis-driven trait-based approaches.

Some of these recommendations have been proposed before (e.g. Chytrý et al., 2014; Kapfer et al., 2017; Morrison, 2016; Vellend, Brown et al., 2013), but in this paper we provide a protocol to actually quantify

the errors. Adopting these recommendations will increase the reliability of the inferences that can be drawn from future resurvey projects. To conclude, we emphasize that people should certainly not be discouraged by the results presented here. Vegetation records going back multiple decades are an invaluable resource for global change research (cf. Verheyen et al., 2017) and researchers should try to get the most out of such research to better understand past and predict future biodiversity changes.

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AUTHOR CONTRIBUTIONS

KV and LB designed the study and led the data analysis and writing of the manuscript. All other authors helped with the data collection, extensively commented on earlier versions of the paper and gave final approval for publication.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

APPENDIX S1 Relationship between plot size and species richness
APPENDIX S2 Interregional variation in the between-record differences in location, richness and composition

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