Published in final edited form as:

Divers Distrib. 2015 March ; 21(3): 322–330. doi:10.1111/ddi.12299.

Vegetation resurvey is robust to plot location uncertainty

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Abstract

Aim—Resurveys of historical vegetation plots are increasingly used for the assessment of decadal changes in plant species diversity and composition. However, historical plots are usually relocated only approximately. This potentially inflates temporal changes and undermines results.

Location—Temperate deciduous forests in Central Europe.

Methods—To explore if robust conclusions can be drawn from resurvey studies despite location uncertainty, we compared temporal changes in species richness, frequency, composition and compositional heterogeneity between exactly and approximately relocated plots. We hypothesized that compositional changes should be lower and changes in species richness should be less variable on exactly relocated plots, because pseudo-turnover inflates temporal changes on approximately relocated plots.

Results—Temporal changes in species richness were not more variable and temporal changes in species composition and compositional heterogeneity were not higher on approximately relocated plots. Moreover, the frequency of individual species changed similarly on both plot types.

Main conclusions—The resurvey of historical vegetation plots is robust to uncertainty in original plot location and, when done properly, provides reliable evidence of decadal changes in plant communities. This provides important background for other resurvey studies and opens up the possibility for large-scale assessments of plant community change.

Keywords

pseudo-turnover; resampling; revisitation; semi-permanent plots; temperate forest; temporal vegetation change

Author contributions: Both authors conceived the ideas and collected the data; M.K. analysed the data and led the writing.

Introduction

Resurveys of historical datasets provide invaluable insights into species distributional shifts and community dynamics in the face of climate and land use change (Leach & Givnish, 1996; Harrison et al., 2010; de Frenne et al., 2014; Grytnes et al., 2014). Essential for any resurvey is the availability of methodologically consistent and spatially explicit historical datasets (Magurran et al., 2010; Vellend et al., 2013). In this respect, historical vegetation plots represent an enormous data source collected by comparable methodology across several continents for over a century (Ewald, 2003; Chytrý et al., 2014; Waller et al. 2012). There are millions of plots already available in electronic databases (Dengler *et al.*, 2011). Vegetation plot resurveys are therefore increasingly used for the assessment of decadal changes in plant communities and subsequent conservation suggestions (Keith et al., 2009; Amatangelo et al., 2011; Verheyen et al., 2012; Kopecký et al., 2013).

Most vegetation plots are, however, non-permanent and their exact locations are not known (Bakker et al., 1996; Chytrý et al., 2014). To relocate such plots, historical maps with plot locations are commonly used (Rooney et al., 2004; Van Calster et al., 2007; Vittoz et al., 2009; Baeten et al., 2010; Naaf & Wulf, 2010). When historical maps are not available, other types of information can be used – e.g. the identification of the forest compartment in which the plot was established (Chytrý & Danihelka, 1993; Hédli, 2004) or the square of the national grid in which the sampling was made (Bennie et al., 2006; Ross et al., 2010). To further increase relocation accuracy, only a site with elevation, slope and aspect similar to the historical plot can be resurveyed (Harrison et al., 2010; Kopecký et al., 2013; McCune & Vellend, 2013). Comparable tree species composition has also been used to relocate the plot within a forest stand, assuming that the time between the surveys is shorter than the turnover of the canopy trees (Chytrý & Danihelka, 1993; Rogers et al., 2008).

Nonetheless, because historical plots are relocated only approximately, resurvey may in fact concern a spatial location with different species composition. This could result in pseudo-turnover – i.e. change in species composition caused by sampling different place (Fischer & Stocklin, 1997). Surprisingly few studies have explored this limitation. Persson (1980) compared temporal vegetation changes on plots resurveyed at the most probable locations of the historical plots with changes on plots shifted five meters apart. Fisher & Stocklin (1997) showed that pseudo-turnover increases with increasing distance between the most probable location of the historical plot and the new relocated plot. Hédli (2004) sampled several new plots for each historical plot and compared vegetation changes observed on the most topographically similar pair of plots with temporal changes of the whole dataset. Finally, Ross et al. (2010) found lower spatial turnover among several new plots established within the probable location of the historical plot than the temporal turnover between all possible pairs of historical and new plots. Collectively these studies indicate that resurvey of non-permanent plots is relatively robust to location uncertainty. However, they addressed temporal pseudo-turnover only in an indirect way by comparing several replicate samples made within the probable area of the historical sample. Their results therefore depend on spatial vegetation heterogeneity within the resurveyed area (Ross et al., 2010).

Here we used a new approach directly comparing vegetation changes between approximately and exactly relocated plots. To explore if robust conclusions can be drawn from resurvey studies despite location uncertainty, we compared temporal changes in species richness, frequency, composition and compositional heterogeneity between exactly and approximately relocated plots in temperate deciduous forests. We hypothesized that compositional changes should be lower and changes in species richness should be less variable on exactly relocated plots, because pseudo-turnover inflates temporal changes on approximately relocated plots. If this is true, the resurveys of approximately relocated plots will provide biased assessment of vegetation changes and their results should be approached with caution.

Methods

Study area

We resurveyed historical vegetation plots in the NW part of the Czech Republic (Fig. 1). We selected this area, because of i) high diversity of semi-natural forest vegetation, ii) anecdotal evidence that forest vegetation substantially changed during the last decades, presumably because iii) forests in this area suffer high nitrogen deposition (up to $2 \text{ g} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ - H nová et al., 2014).

The climate is temperate, with 6-7 °C mean annual temperature and 550-600 mm of mean annual precipitation (Tolasz et al. 2007). The relief is highly variable (200-800 m a.s.l.), with characteristic volcanic hills rising from the sedimentary plateau (Fig. 1).

The diversity of semi-natural forest vegetation reflects this environmental heterogeneity. Oak-hornbeam forests dominated by *Quercus petraea* and *Carpinus betulus* cover the plateau and the lower parts of the hills, while beech forests (*Fagus sylvatica*) dominate on hill tops and northern slopes. Thermophilous oak forests with *Quercus pubescens* occur mainly on southern slopes, and ravine forests (*Tilia cordata* and *platyphyllos*, *Acer pseudoplatanus* and *platanoides*, *Ulmus glabra*) cover steep slopes and screes. Alluvial forests with *Fraxinus excelsior* and *Alnus glutinosa* occur along the streams.

Data collection

We resurveyed historical vegetation plots stored in the Database of Czech Forest Classification System (Zouhar, 2012). This database contains over 30 000 plots sampled with comparable methodology in the Czech Republic since the 1950s. The aim of the original sampling was to document forest vegetation heterogeneity and to provide a basis for forest type classification. In the field, sampling followed a standardized protocol, which included the permanent marking of the central tree within the plot (Mráz & Samek 1957). Simultaneously, plot location was indicated on a forestry map usually with a spatial resolution of 1:10 000.

We retrieved all plots sampled in the study region before 1980 from the database. For resurvey, we selected plots originally sampled by a single observer (J. Smejkal) in 1972-1973. To relocate these plots, we used: 1) geographic coordinates of plot location on the historical map, 2) plot elevation, slope and aspect and 3) tree species composition. In the

field, we navigated to the approximate location of each plot with a GPS receiver and then thoroughly searched for places with corresponding topography and tree species composition. We also searched for the original mark painted on the central tree (Fig. 1). If we found the mark, we resurveyed the same site around the central tree. In other cases, we sampled the most probable site according to the information from the original survey.

In 2013, we resurveyed all plots originally established in semi-natural broadleaf forests which were not clear-cut between the surveys. From 69 resurveyed plots, we exactly relocated 24 plots. The remaining 45 plots were relocated only approximately (Fig. 1). We resurveyed the plots in the same season and used the same plot area as in the original survey (450 or 500 m²). Within each plot, we listed all vascular plant species, assigned them to vertical layers (e.g. tree, shrub, herb) and estimated their cover-abundance according to the Zlatník scale used during the original survey (Zlatník 1953). The Zlatník scale has 11 ordinal classes, the first two express species abundance (less than 3 individuals; more individuals but with cover below 1 %), while the rest express species cover (up to 5, 15, 25, 37, 50, 62, 75, 87 and 100 %).

Data analysis

To explore whether the uncertainty in plot location affects the assessment of temporal changes in the forest herb layer, we compared changes in species richness, frequency, composition and compositional heterogeneity between exactly and approximately relocated plots. First, we standardized plant nomenclature according to Kubát et al. (2002). Where species identification was uncertain, we combined taxa at the aggregate or genus level. We also transformed the ordinal classes of the Zlatník scale to species percentage cover. We converted the two lowest classes as 1 and 2 % and all other classes as percentage midpoints of the respective class.

Species richness—To test if the temporal changes in the number of taxa present within the plot differ in magnitude or variance between exactly and approximately relocated plots, we used a two-sample Kolmogorov-Smirnoff test implemented with *ks.test* function in R (R Core Team 2013).

Species frequency—To assess whether relocation uncertainty bias changes at the species level, we correlated temporal changes in species frequency on exactly and approximately relocated plots. From the total species pool (N=243), we selected species which occur in more than one sample in both plot types (N=98). To test whether these species changed comparably between plot types, we used the Pearson correlation coefficient.

Species composition—To explore if species turnover differs between exactly and approximately relocated plots, we tested the interaction between type of plot and survey period. To calculate temporal turnover in species identities, we used the incidence based Simpson index (Lennon *et al.*, 2001). To calculate temporal turnover in species proportions, we used the abundance based Bray-Curtis index calculated from species cover data standardized by sample totals.

We used permutation-based MANOVA (Anderson, 2001) to test the interaction between type of plot and survey period. To correctly partition type III sum of squares, we used *anova.2way.unbalanced* R-function and tested the interaction by permutation of the raw data (Anderson & Legendre, 1999). Following Borcard et al. (2011, pp. 185-188), we checked the test assumption of homogeneity of the variance-covariance matrices with *betadisper* R-function from the *vegan* package (Oksanen et al. 2013).

To visualize compositional changes, we performed non-metric multidimensional scaling (NMDS) in two dimensions. We performed global NMDS separately on Simpson and Bray-Curtis dissimilarity matrices using the *monoMDS* R-function from the *vegan* package.

Compositional heterogeneity—To explore if compositional heterogeneity changes differ between exactly and approximately relocated plots, we compared temporal changes in plot distances to the multivariate centroid of all plots from the same survey (Anderson *et al.*, 2006). First, we projected Simpson and Bray-Curtis dissimilarity matrices into euclidean space and extracted plot distance to the group centroids (spatial medians) using *betadisper* R-function. Then, we tested the interaction between type of plot and survey period using the test for homogeneity in multivariate dispersion (Anderson, 2006) implemented with *anova.2way.unbalanced* R-function.

Results

The resurvey of approximately and exactly relocated plots provided a comparable assessment of temporal vegetation changes (Table 1). The variability and magnitude of species richness changes was not higher on approximately relocated plots (Fig. 2).

The frequency of individual species changed similarly on exactly and approximately relocated plots ($R = 0.72$, $t = 10.04$, $p < 0.0001$; Fig. 3).

Despite considerable species turnover (Fig. 4), the compositional changes were not substantially higher on approximately relocated plots (Fig. 5). The magnitude of changes in compositional heterogeneity was not higher on approximately relocated plots (Fig. 6).

Discussion

Our results suggest that temporal changes inferred from vegetation plot resurveys are robust to uncertainty in original plot location. This is important as resurvey studies are increasingly used to assess decadal vegetation changes and provide management and conservation recommendations (Bergamini et al., 2009; Kopecký et al., 2013; Meyer et al., 2013). The uncertainty in plot relocation - potentially inflating temporal changes - has been frequently used as an argument against resurvey studies. However, our results showed that the resurvey of semi-permanent historical plots can provide vegetation change assessment comparable to permanent plots. This provides important background for other resurvey studies and supports their conclusions. Moreover, our results indicate that permanent plots no longer marked in the field can be successfully relocated. This will allow vegetation change assessment over longer time-period that is usually possible with intensive but short-term data from vegetation monitoring programs (Bakker et al., 1996; Chytrý et al., 2014).

In our study, we assessed the importance of imprecise plot relocation, but it is not the only factor that could cause compositional pseudo-differences between resurveyed plots. The observer is usually not the same for different sampling periods and this can introduce temporal pseudo-differences through subjective cover estimation, plant misidentification or overlooking (Lepš & Hadincová, 1992; Scott & Hallam, 2002; Archaux et al., 2009; Vittoz et al., 2010). Within season vegetation variability and among season fluctuations can also contribute to the compositional pseudo-turnover (Kirby et al., 1986; Brunet & Tyler, 2000; Vymazalová et al., 2012). These biases are nevertheless common to all repeated samples, both from approximately and exactly relocated plots. Our results are therefore not affected by them, because - if they are present within our dataset - they are the same for samples from approximately and exactly relocated plots. However, the issue of these possible pseudo-differences between resurveyed vegetation plots needs to be addressed in the future.

Plot relocation

To relocate the plots, we used geographic coordinates extracted from historical maps, local topography and species composition of the tree layer. While historical maps and terrain morphology have been used frequently, tree species composition has been used only rarely (Chytrý & Danihelka, 1993; Rogers et al., 2008). In the field, we found the historical mark only after close examination of the site with the tree species composition corresponding to the historical one. Especially useful were admixture tree species in stands with one dominant species (e.g. a single linden in an otherwise oak-dominated forest). We therefore encourage researches to use tree species composition as an additional criterion for plot relocation in the field.

This of course assumes that the time between the surveys is shorter than the turnover of the canopy trees. However, this is not a problem for most studies as only few resurveys span more than six decades (Keith et al. 2009; Newton et al. 2012; Šebesta et al. 2011). The importance of this limitation will nevertheless increase in the future.

The second assumption is that no major canopy disturbance occurred between the surveys. This is not an important limitation for most studies, either, because such disturbance-affected plots are usually *a priori* discarded from the resurvey to avoid successional young stages with their distinct species composition (Hédl, 2004; Wild et al., 2004; Wiegmann & Waller, 2006).

In line with this common practice, we resampled only stands that were not clear-cut and replanted between the surveys. Theoretically, we should have found marked trees on all plots. In reality, we found the marked tree only on one third of all resurveyed plots. This can be attributed to the surveyor not marking the tree, our failure to find the mark, the death of the marked tree or occasional thinning. We think that in most cases thinning is the probable explanation, because sanitary thinning is often performed within the region and we found some stumps both on exactly and approximately relocated plots.

Datasets for resurvey

Careful selection of historical datasets with sufficient information is essential for any resurvey. Therefore we stress that our results can be specific for our study area, data source

or even sample size and we encourage other researchers to carry out similar comparisons. We resurveyed plots scattered over 100 km² of a topographically diverse landscape and this resulted in high species turnover among resurveyed plots. The relocation-driven pseudo-turnover should be lower in regions with less variable vegetation (Ross et al. 2010). Our results therefore suggest that resurveys are robust to relocation uncertainty even in heterogeneous regions.

Another interesting question is the effect of plot size on compositional pseudo-turnover between resurveys. Our plots were larger than the most common size used for sampling forest vegetation in Europe (Chytrý & Otýpková 2009). Many resurveys used substantially smaller plots (Verheyen et al. 2012; Vellend et al. 2014). It is therefore possible that the effect of relocation error will be higher in resurveys of these smaller plots, because smaller plots can capture more fine-scale vegetation variability (Reed et al. 1993).

We resurveyed plots extracted from the Database of Czech Forest Classification System. Most historical plots stored in this database have been collected with comparable sampling protocols. We are therefore confident that the results from our study area can be generalized to other data stored in this database. We found all exactly relocated plots within 60 m from the original coordinates, and the mean distance between original coordinates and the marked tree was only 27 m. This indicates that plot geographic coordinates are surprisingly accurate given the combined uncertainty of the original plot marking in the map and the geographic coordinates of the marked tree measured with a basic GPS receiver (Johnson & Barton, 2004; Piedallu & Gégout, 2005).

The understanding of temporal patterns in biodiversity is limited by the availability of long-term, large-scale and high-resolution data (Dornelas *et al.*, 2013). The data stored in the Database of Czech Forest Classification System have all these characteristics (Zouhar 2012). Moreover, our study showed that their resurvey provides results robust to location uncertainty. This highlights their potential for resurvey studies on the national scale and we plan to move in this direction in the future.

Contrary to forest plot databases, most vegetation databases are based on legacy data from local phytosociological studies (Dengler *et al.*, 2011). These local datasets have been collected with various research aims and survey designs, which substantially reduce their utility for large-scale studies of vegetation change (Chytrý *et al.*, 2014). Moreover, historical phytosociological relevés usually have only vague descriptions of plot location (Dengler *et al.*, 2011). This is in sharp contrast with the standardized sampling performed in forestry over large regions (Thomas et al., 2009; Bertrand et al., 2011; Zhu et al., 2012). Therefore we argue that resurveys of forest plot databases can be used for vegetation change assessment at a scale that is not possible with legacy data from traditional phytosociological studies. This would provide large-scale and community-wide insights into decadal changes in plant species diversity and distribution, while maintaining all details of spatially explicit plot data.

Conclusions

Our results suggest that the resurvey of historical plots - despite the uncertainty in original plot location - represents a robust way to infer temporal vegetation changes. This provides important background for other resurvey studies and opens up the possibility for large-scale assessments of plant community change.

Acknowledgements

We thank Radim Hédli, Jesse M. Kalwij, Péter Szabó and three anonymous reviewers for useful comments. We thank Péter Szabó also for language revision and Václav Zouhar for his help with the forestry database. The research leading to these results has received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013)/ERC Grant agreement no 278065. Additional funding was provided by projects RVO 67985939 and CZ.1.07/2.3.00/20.0267 with the financial contribution of the EC and the state budget of the Czech Republic.

Biosketches

Martin Kopecký is fascinated by the nature changing in time and space. In his research, he is trying to uncover patterns of plant community changes and the processes that have caused them.

Martin Macek focuses on the links between plant niches and communities in forests. He conducts his research in context of human induced changes as well as nature disturbances.

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Figure 1. Location of the study area within Central Europe; landscape distribution of exactly (red squares) and approximately (blue dots) relocated plots; and original mark - yellow stripe - on the central tree within the plot.

Figure 2.

Species richness changes are not more variable on approximately relocated plots. Ridge plots show the density distribution of species richness changes within each plot type, the species richness change on individual plots (short vertical lines), the means for each plot type (thick vertical lines) and the 95% bootstrapped confidence interval (shaded area) around the overall mean (dashed line). To reduce overplotting, the individual values were slightly shifted.

Figure 3.

Frequency of individual species changed similarly on exactly and approximately relocated plots. The dots represent temporal change in individual species frequency and the line represents linear relationship fitted to the data.

Figure 4.

Species composition shifted similarly on exactly (red squares) and approximately (blue dots) relocated plots. The filled symbols represents samples from the original survey, the lines connect both samples from the same plot and the ends of the lines represent samples from the resurvey. The sample configuration from nonmetric multidimensional scaling (NMDS) was centred and rotated by principal component analysis.

Figure 5.

Species composition changed substantially - but comparably - on exactly and approximately relocated plots. Ridge plots show the density distribution of turnover within each plot type, the turnover on individual plots (short vertical lines), the means for each plot type (thick vertical lines) and the 95% bootstrapped confidence interval (shaded area) around the overall mean (dashed line). To reduce overplotting, the individual values were slightly shifted.

Figure 6.

Compositional heterogeneity changes were not higher on approximately relocated plots. Ridge plots show the density distribution of compositional heterogeneity changes within each plot type, the changes on individual plots (short vertical lines), the means for each plot type (thick vertical lines) and the 95% bootstrapped confidence interval (shaded area) around the overall mean (dashed line). To reduce overplotting, the individual values were slightly shifted.

Table 1

Mean temporal changes in species richness, composition and heterogeneity in exactly and approximately relocated plots. The differences in temporal changes were evaluated by Kolmogorov-Smirnoff test (species richness), permutational MANOVA (species composition) and test of multivariate homogeneity of group dispersions (compositional heterogeneity).

	Plot relocated		Statistics	p-value
	exactly	approximately		
Species richness	-0.83	0.00	0.153	0.82
Composition (Simpson)	0.37	0.41	0.629	0.23
Composition (Bray-Curtis)	0.56	0.59	0.489	0.48
Heterogeneity (Simpson)	0.02	-0.02	0.898	0.17
Heterogeneity (Bray-Curtis)	-0.01	-0.03	0.696	0.28