

Combining biodiversity resurveys across regions to advance global change research

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Abstract:	More and more ecologists have started to resurvey communities sampled in earlier decades to determine long-term shifts in community composition and infer the likely drivers of the ecological changes observed. However, to assess the relative importance of, and interactions among, multiple drivers

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	joint analyses of resurvey data from many regions spanning large environmental gradients are needed. In this paper we illustrate how combining resurvey data from multiple regions can increase the likelihood of driver-orthogonality within the design and show that repeatedly surveying across multiple regions provides higher representativeness and comprehensiveness, allowing us to answer more completely a broader range of questions. We provide general guidelines to aid implementation of multi-region resurvey databases. In so doing, we aim to encourage resurvey database development across other community types and biomes to advance global environmental change research.

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Combining biodiversity resurveys across regions to advance global change research

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Abstract

More and more ecologists have started to resurvey communities sampled in earlier decades to determine long-term shifts in community composition and infer the likely drivers of the ecological changes observed. However, to assess the relative importance of, and interactions among, multiple drivers joint analyses of resurvey data from many regions spanning large environmental gradients are needed. In this paper we illustrate how combining resurvey data from multiple regions can increase the likelihood of driver-orthogonality within the design and show that repeatedly surveying across multiple regions provides higher representativeness and comprehensiveness, allowing us to answer more completely a broader range of questions. We provide general guidelines to aid implementation of multi-region resurvey databases. In so doing, we aim to encourage resurvey database development across other community types and biomes to advance global environmental change research.

Key-words: legacy data, (quasi-)permanent plots, community ecology, ground layer vegetation, temperate forest

1. Introduction

Increasing human impacts on the environment have large and pervasive effects on the composition and functioning of ecosystems (Millenium Ecosystem Assessment 2005). This makes it important to document and understand how ecosystems and communities are changing and to determine how the multiple drivers of global change interact. Without such knowledge, we are unable to develop appropriate strategies for the effective conservation and restoration of biodiversity and to maintain desired ecosystem functions.

To improve our understanding of how multiple global change drivers affect ecosystems, we should combine different methods (Luo et al. 2011). Quantifying how ecosystems and communities vary along environmental gradients is an important source of information in this respect (e.g. Newbold et al. 2015), complementing knowledge gained from experiments and modelling studies (cf. Luo et al. 2011). Environmental gradient studies can give information on ecosystem responses to multiple drivers across space, and can also be used to infer how ecosystems may potentially respond to temporally varying drivers. However, such space-for-time approaches rely on many assumptions (e.g. Walker et al. 2010). Repeat observations of the same community over time to quantify how communities are changing are therefore invaluable additional sources of information (e.g. Tingley & Beissinger 2009, Dornelas et al. 2012), particularly when data extend to several decades or longer, as more reliable and informative signals to estimate the nature and rates of change can be obtained (cf. Magnuson 1990; Pauly 1995).

More and more ecologists have started to resurvey communities sampled in earlier decades to determine long-term shifts in community composition and infer the likely drivers of the ecological changes observed. Plant ecologists now use vegetation data from early to mid-20th century vegetation descriptions to examine long-term changes in these communities (see e.g. Bakker et al. 1996 for an earlier discussion on the topic). Many examples from other communities exist as well

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2 46 (e.g., birds: Tingley and Beissinger 2013; butterflies: Nieto-Sánchez et al. 2015; small-mammal
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4 47 communities: Moritz et al. 2008; zoobenthos: Olsson et al. 2013).
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7 48 However, most resurvey studies have worked with data collected in single regions and their utility
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10 49 is limited if we are to understand the importance of the multiple, often interacting, global-change
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12 50 drivers that affect plant and animal communities. These drivers vary at multiple spatial and
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14 51 temporal scales and often covary in space and time. Proper assessments of the relative
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16 52 importance of multiple drivers and of the interactions among them require us to analyse resurvey
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18 53 data from multiple regions, spanning large environmental gradients and multiple geographic
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24 55 In this paper we provide arguments as to how pooling resurvey data from multiple regions realises
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26 56 the potential to make major contributions to the understanding of community dynamics and
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28 57 response to various interacting environmental changes. We illustrate our arguments with
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30 58 published results from long-term resurveys of temperate forest ground layer vegetation, and
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32 59 share lessons to enable database development and data retention in other community types and
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34 60 biomes. Our approach serves as an example of data sharing and collaboration (Wolkovich et al.
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36 61 2012, Mills et al. 2015) and furthermore provides an example of how to make best use of legacy
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38 62 datasets, which are often abandoned and at risk of being lost (see also Vellend et al. 2013).
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47 64 **2. The added value of multi-region community resurvey data: representativeness,**
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52 66 Well-reasoned criteria for dataset inclusion are needed to turn a collection of datasets into a
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54 67 powerful ecological research platform. In this section we therefore start by defining the main
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56 68 features of resurvey datasets suitable for inclusion in a multi-region analysis and then compare
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69 how a collection of resurvey datasets performs compared to multi-region experiments and *a priori*
70 designed community monitoring networks.

71 We define a resurvey data set as a collection of community surveys sampled at multiple locations
72 within a defined region and across at least two points in time. The two time points typically span a
73 period of at least several decades in order to obtain a true long-term perspective on
74 environmental and community change; i.e. *the* unique, invaluable feature offered by legacy
75 datasets. A region is defined here as a geographic entity with more or less similar site conditions,
76 including climate, major soil types and levels of atmospheric nitrogen deposition. Regions are
77 defined this way since the main objective of multi-region resurvey data analyses is to quantify the
78 (interactive) effects of multiple drivers which often vary at different scales. For instance, climate
79 change generally plays out at larger spatial scales, whereas management changes can vary among
80 locations within a single region. However, the combined outcome of both drivers will ultimately
81 determine changes in the local microclimate and the resulting changes in community composition
82 (see Fig. 1 for an example). A combination of multiple regions with multiple resurveyed locations
83 within each region is therefore a key design feature of a research platform that aims at
84 understanding long-term community changes. Besides these general criteria, also specific criteria
85 for the inclusion of datasets in the research platform need to be defined so that the platform
86 resembles *a priori* community monitoring networks with a standardized design (Table 1).

87 Such a multi-region network of community resurvey data scores well for all three fundamental
88 design criteria for ecological research platforms, notably comprehensiveness, representativeness
89 and orthogonality (Nadrowski et al. 2010, Baeten et al. 2013; Fig. 2). "Comprehensiveness" in this
90 paper relates to the spectrum of ecological questions that can be addressed with a particular
91 research platform. "Representativeness" refers to the relevance of analysed results for sites that
92 were not included in the investigation. Finally, the "orthogonality" of the platform refers to its

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2 93 ability to disentangle the separate effects of each environmental driver on the response variable(s)
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4 94 under study. Most obviously, the representativeness generally increases when an increasing
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8 96 will more likely fit within the environmental envelope spanned by the platform. This should lead to
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10 97 more reliable inference. The spatiotemporal replication of community data (i.e. resurveys in
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12 98 multiple locations in multiple regions) strongly increases the likelihood of orthogonality within the
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14 99 design. It should be noted that orthogonality and representativeness are not entirely independent
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16 100 in this case: the inclusion of multiple regions is a necessary condition to increase orthogonality for
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18 101 drivers varying at large spatial scales and this will simultaneously increase the representativeness.
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21 102 Finally, repeatedly surveying broadly across multiple landscapes or regions also results in high
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25 104 potentially unanticipated ones.
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31 105 In addition, long-term multi-region resurveys have the ability to complement the outcomes of
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33 106 globally distributed experiments with environmental manipulations, such as nitrogen addition (cf.
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35 107 Fraser et al. 2013, Borer et al. 2014; Fig. 2). Although experiments typically score higher on the
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37 108 orthogonality axis, they reduce representativeness and often comprehensiveness by using
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39 109 simplified communities and often extreme ('shock') treatments (e.g. a sudden shift from low to
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41 110 high temperature regimes) with a limited number of treatment levels. Furthermore, treatment
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43 111 responses are rarely monitored for more than a few years. These elements constrain the spectrum
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45 112 of questions that can be addressed with experiments and hence their comprehensiveness. Making
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47 113 best use of long-term resurveys from multiple sites as a complement to experimental approaches
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49 114 therefore responds to calls for more integrated approaches to better understand the effects of
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51 115 global changes on complex ecological communities and ecosystem functions (Luo et al. 2011, De
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53 116 Frenne et al. 2013) (see Frerker et al. 2014 for a good example).
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Parallel to the rise of globally distributed experiments, also more and more *a priori* designed community monitoring networks across large environmental gradients are being established. They include top-down designed networks such as the European Level I and II monitoring networks of air pollution effects on forests (<http://icp-forests.net/>) and the UK Countryside Survey (<http://www.countrysidesurvey.org.uk>). Multi-region community resurvey networks with a more bottom-up approach, in which regions participate on a voluntary basis, have emerged as well. The GLORIA-network (Pauli et al. 2015) can serve as a prime example. The network applies a highly standardized 'Multi-Summit Approach' to survey alpine biodiversity and vegetation patterns on four mountain summits per target region. The results of this observation network help us to better understand the response of alpine biota to climate change (see e.g. Pauli et al. 2012). The first plots were established in 2001 and have been resurveyed at regular intervals since then. Although these multi-region monitoring networks have already produced very valuable results and will certainly continue do so in the future, they have rarely been established more than one or two decades ago and therefore well after the rise in many anthropogenic pressures. Since insights in longer term changes are badly needed (cf. Pauly 1995), attempts should be made to make best use of archived community survey data collected in a more distant past.

In the next section, we illustrate how to put together a network using legacy community resurvey data by introducing forestREplot. In addition, we synthesize already published results from forestREplot to show how new insights can be developed and more general conclusions reached.

3. Putting long-term multi-region resurveys into practice: the forestREplot network as an example

Resurveys of long-term (quasi-)permanent plots are particularly appropriate for communities that exhibit slow dynamics, such as ground layer communities in forests. These plant communities

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2 141 often show delayed responses to environmental **changes: the** long life span of many ground layer
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4 142 species (Ehrlén and Lehtilä 2002) promotes remnant populations and extinction debts (Eriksson
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6 143 1996, Vellend et al. 2006), while slow immigration rates can lead to colonization credits (Verheyen
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8 144 et al. 2003). Since the ground layer in temperate forests comprises the majority of plant diversity
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10 145 in these systems and has an important impact on their functioning (Gilliam 2007), it is important
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12 146 to document the long-term changes in the ground layer composition and diversity and to
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14 147 understand the drivers that underlie these changes. Changes documented in forest understories
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16 148 may also serve as early warnings of impacts to even slower canopy dynamics.
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21 149 The ‘forestREplot’ network (www.forestreplot.ugent.be) brings together standardized ground
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23 150 layer vegetation resurvey plots collected in natural or semi-natural forests in different regions
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25 151 across Europe and North America (Verheyen et al. 2012, De Frenne et al. 2013, Baeten et al. 2014,
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27 152 Bernhardt-Römermann et al. 2015). Table 1 gives an overview of the criteria used for dataset
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29 153 inclusion in forestREplot. The database currently consists of 55 datasets and nearly **3000 pairs of**
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33 155 Depauw and Maes 2015 for more info and Appendix I for an overview).
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38 156 The network aims to: (i) collect and archive datasets of resurveyed vegetation plots in temperate
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42 158 questions in ecology, with a specific focus on the ground layer and the impacts that various, often
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44 159 interacting, global change drivers have on this layer. In many respects, the design and
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48 161 experiments outlined by Fraser et al. (2013) and Borer et al. (2014).
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53 162 Here we illustrate with forestREplot how multiple resurvey datasets can address a broad spectrum
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55 163 of ecological questions (i.e. the comprehensiveness), with results being representative for real-
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57 164 world changes in temperate forest communities (i.e. the increased representativeness).
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Furthermore, we show how the approach may disentangle the relative importance of multiple drivers of change in the ground layer of forests (i.e. the increase in orthogonality).

3.1 Comprehensiveness

To quantify the spectrum of ecological questions that can be addressed with multi-site resurvey data, here shown using the forestREplot example, we performed a two-step survey among 32 participants of the first forestREplot workshop organised in December 2014 in Ghent, Belgium. All participants to the workshop were data contributors to the forestREplot-database. Prior to the meeting, the workshop organizers (K.V., L.B., L.D.P., M.B.-R., P.D.F., R.H. and S.M.) quantitatively assessed which of the current 100 fundamental questions in ecology (as listed by Sutherland et al. 2013) could be answered with the forestREplot database by attributing a score between one (not suitable) to three (very suitable) to all questions. This resulted in a subset of 42 fundamental questions of the original Sutherland et al. 2013 list with a score ≥ 2 . Next, we asked the workshop participants to score the potential of the forestREplot database to answer these 42 questions. The top ten questions which had the highest probability of being scored very suitable can be found in Table 2. The full list with question and scores can be found in Appendix II.

3.2 Representativeness

As we amass resurvey data from more sites, spread over larger regions, we gain a clearer picture of which changes are local or idiosyncratic to a few locations and which reflect more general and widespread changes (Fig. 2). However, results from any given database are clearly bounded by the variation within the set of species, communities, and environmental conditions present within the database. Resurvey data included in forestREplot, for instance, only come from semi-natural and

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2 188 natural forests (see Depauw and Maes 2015). Furthermore, forestREplot is merely a collection of
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4 189 datasets and not a designed monitoring program based on probabilistic sampling, such as National
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6 190 Forest Inventories (NFI), which reduces the representativeness and makes the statistical analyses
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8 191 more complicated. For instance, many of the first surveys were made for phytosociological
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10 192 purposes, meaning that plot locations are not entirely randomly chosen. These limitations have to
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12 193 be acknowledged when using the data (cf. Holeksa and Woźniak 2005, Michalcova et al. 2011). On
13
14 194 the other hand, most monitoring programs designed to be representative do not (yet) span long
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16 195 time periods (but see Hedwall and Brunet 2016). Furthermore, the spatial sampling resolution in
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18 196 these monitoring programs is often rather low so that smaller scale changes risk going undetected.
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26 198 *3.3 Orthogonality*

29 199 Single-region studies have shown that ground-layer vegetation in temperate forests responds
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31 200 sensitively to global change drivers, including forest management, atmospheric nitrogen
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33 201 deposition, and climate change (Table 3). However, these studies often do not show consistent
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35 202 responses, as exemplified for species richness in Table 3. Furthermore, community responses may
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37 203 not be monotonic over longer environmental gradients. To analyse the orthogonal and interacting
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39 204 effects of these drivers on biodiversity, it is necessary to either include many sites and studied
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41 205 factors within a single, large-scale, study, or to combine results from several single studies in joint
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43 206 analyses.
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49 207 For instance, Verheyen et al. (2012) presented a meta-analysis of 23 local-scale resurveys from
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51 208 across Europe that focused on the contribution of atmospheric N deposition versus changes in
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53 209 forest management to explain changes in herb layer composition. Shifts in vegetation composition
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55 210 seemed mainly related to management-related alterations in the canopy structure and
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57 211 composition, independent of the N deposition.
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An additional study exploring the mechanisms driving temporal changes in biodiversity was performed by Bernhardt-Römermann et al. (2015). Using 39 data sets of resurvey data on forest understory communities across Europe, temporal changes in species richness were related to environmental data at multiple spatial scales (continental, regional, local). These joint analyses were designed to relate temporal changes in species richness with i) across-site variation in environmental conditions at the time of the initial vegetation survey (i.e. baselines) and ii) temporal changes in environmental conditions between vegetation surveys. No significant and directional changes in local diversity were found, although there was considerable across-site variation, corroborating earlier findings (Verheyen et al. 2012, Vellend et al. 2013). This across-site variation was determined by both local and regional scale drivers (temporal changes in local stand structure and game density). Most excitingly, strong evidence was found that pre-survey levels of N deposition determined subsequent changes in biodiversity. Recently, Simkin et al. (2016) confirmed the existence of context-dependent effects of N-deposition on plant diversity using a large dataset from the US.

Thirdly, increased dominance of warm-adapted plant species (so-called 'thermophilization') as a result of climate warming has been identified across several ecosystems (Bertrand et al. 2011, Gottfried et al. 2012). However, De Frenne et al. (2013) found that this thermophilization was lowest in forests that had become denser over time across Europe and North America, suggesting that reducing management intensity to increase shading can buffer the impacts of global warming (cf. also De Frenne et al. 2015).

These three examples show how multi-region analyses can increase orthogonality compared to single-region studies.

4. Challenges associated with resurvey data

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2 236 Despite the great potential that combining long-term resurvey data from multiple regions holds,
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4 237 some important challenges remain, both at the level of the individual resurvey studies and when
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6 238 trying to combine them.
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10 239 Sources of unwanted variability or bias in resurvey studies have received considerable attention in
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12 240 the scientific literature (e.g. Tingley and Beissinger, 2009). Taking the example of vegetation
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14 241 resurveys, studies have been performed to quantify the level of bias introduced due to (1)
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16 242 relocation errors (e.g. Fischer & Stöcklin 1997, Kopecký and Macek 2015); (2) species detectability,
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18 243 observer effects and sampling exhaustiveness (Archaux et al. 2006, Vittoz and Guisan 2007,
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20 244 Milberg et al. 2008); (3) taxonomic inconsistencies (Jansen and Dengler 2010); (4) and to
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22 245 differences in recording dates (Van Calster et al. 2008). Recently, Semboli et al. (2014) highlighted
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24 246 a new source of bias, notably a changing vegetation composition after multiple resurvey visits due
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26 247 to, among others, trampling effects. Many of these biases are not easy to solve, particularly when
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28 248 the first surveyors are no longer around. Hence the need for a robust archiving of survey data so
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30 249 that at least future generations of researchers are not confronted with these issues (see Box 1).
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36 250 When multiple datasets are combined, additional challenges arise that relate to differences in
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38 251 baselines (e.g. due to historical land use or air pollution legacies), variation in the time interval
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40 252 between the surveys and variation in the sampling protocols used. For instance, if there is
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42 253 covariation of plot sizes or the time interval between the surveys with environmental changes of
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44 254 interest, then the observed community changes might be principally caused by species-area or
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46 255 temporal effects. These issues require serious attention from the start of any analysis, for
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48 256 instance, by setting strict inclusion criteria for resurvey datasets with deviating baseline
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50 257 conditions, resurvey time intervals, sampling unit properties or internal heterogeneity.
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55 258 Even if studies are carefully selected based on the methods used to gather the community data,
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57 259 the nature of the temporal data involves several challenges from an analytical point of view. For
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time series data similar difficulties such as measurement errors and temporal autocorrelation were identified (Dornelas et al. 2012), but the clever analytical strategies to deal with these do not always easily translate into solutions for typical resurvey studies that provide data for only two time points. For instance, the nature of a temporal trend (e.g., accelerating decrease in diversity) can be quantified with statistical models that account for temporal autocorrelation, but only if sufficient time points are available. Previous studies have used (log) response ratios of old and recent plot values to compare between datasets in a meta-analytical framework (e.g. Verheyen et al. 2012, Bernhardt-Römermann et al. 2015). But while this allows standardizing for particular sampling differences between datasets (e.g. plot size), it does not account for variation in the time interval between surveys, unless assumptions are made about the nature of the temporal change (e.g. a (log)-linear response over time; Verheyen et al. 2012). Finally, analyses usually include predictors of change at different scales (plot, study, cross-study) and typically require multilevel models (Qian et al. 2010).

5. Outlook

The challenges described above should not discourage researchers from seeking to recover historical legacy data, from working to properly document and archive the data (**Box 1**), and from doing the matched resurveys necessary to document long-term ecological change. Many valuable historical community descriptions exist that can be used to generate and test novel insights into ecological change. Furthermore, insights will be deeper and more general when we can combine data from multiple regions and analyse the results in a comparative context. In this paper, we used the forestREplot network as an example of the power that long-term resurvey data have for addressing how communities are responding to a broad range of environmental factors. However, we should bear in mind that forestREplot focuses only on forest ground layer communities in

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2 284 natural and semi-natural temperate forests. We therefore encourage the development of more
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4 285 multi-region resurvey databases for other community types and biomes, as well as new modes of
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6 286 (trait-based) analysis. These will increase the number and nature of the comparisons we can make,
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8 287 allowing, in turn, to test a wider range of hypotheses and reach more general conclusions. Over
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10 288 time, such tests, performed on replicated sets of regions across many distinct biomes, will allow to
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12 289 more fully assess the several, often interacting, effects of forces driving ecological change.
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Box 1: Maintaining the resource. Towards a publicly accessible data and metadata archive for resurveys

Addressing important ecological questions on ecosystem responses to environmental change through the use of long term data requires the data to exist in the first place, necessitating support for long term ecological research infrastructure and its integration e.g. the European Platform for Biodiversity Research Strategy, the International Long Term Ecological Research Network. It then requires indefinite survival of these high quality data and, equally important, their accompanying metadata, and finally, these data to be accessible for analysis. Here, we discuss the need for metadata, the requirement for scientists to know what data are available where, and analysis implications, referring to our experience with vegetation resurveys and forestREplot in particular; the lessons, however, are applicable to all ecological resurveys, and long-term data in general.

In the past, ecological researchers tended to maintain their own records, passing on data and its context to a relay of successors. However, relay batons have been dropped, successors have not emerged, records have consequently been lost or destroyed, and ‘information entropy’ has ensued (Michener et al. 1997). To avoid unnecessary data loss, well documented procedures to preserve data with accompanying metadata are required (Figure I). Of fundamental importance is preservation of the metadata – defined as representing the higher level information or instructions that describe the content, context, quality (e.g. data anomalies / missing data), structure and accessibility of a specific dataset (Michener et al. 1997). In the context of vegetation resurveys, for example, this includes detailed descriptions of cover estimation to enable spatial and temporal comparisons and clear identification of taxonomic authorities and its context of use (see Wiser 2016 for an interesting discussion of issues associated with nomenclatural/taxonomic changes across space and time). In forestREplot, metadata information is gathered systematically

by asking contributors to fill in site and plot information sheets, which characterise the location, land use history, soil type and management disturbance between surveys, while taxonomic harmonization uses the PLANT LIST (www.theplantlist.org/) and, if unresolved there, the Euro+Med PlantBase (www2.bgbm.org/EuroPlusMed/). Without such metadata, and careful integration of primary data, understanding and analyses would be impossible (see also Borer et al. 2014).

The fundamental ecological research questions that broadly distributed vegetation resurveys (and other ecological approaches) also require knowing what data are available where. Vegetation databases are rapidly developing at regional and global levels, and can be identified through the Global Index of Vegetation Plot Databases: www.givd.info. Automated retrieval and checking systems are increasingly being utilised to speed up data acquisition, checking and ‘wrangling’ of data (i.e. their integration) to allow analyses, within the broad field of ecoinformatics (Madin et al. 2007, 2008, Michener and Jones 2012, Wiser 2016). Such efforts complement network initiatives such as forestREplot, which have grown informally and identified separate datasets that have been manually integrated to allow synthetic analyses (e.g. Verheyen et al. 2012, De Frenne et al. 2013). All these approaches will be in vain, however, without the required archiving of resurvey data and metadata in the first place.

Ultimately, archiving may be best incentivised for scientists through publication of the data (in “data papers” rather than typical research articles) using established channels of automated and semi-automated data checking culminating in peer review (Costello et al. 2013). Organisations such as the Global Biodiversity Information Facility can aid this publication and archiving endeavour. Otherwise the contemporary situation (where 80% of scientists want to access data created by others but only 20% have actually shared their data) may continue to persist and

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2 538 valuable opportunities to answer fundamental ecological questions may be lost as time-poor
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4 539 scientists prioritize publication over making data available (Costello et al. 2013).
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7 540 Archiving may also be encouraged by recent policies to mandate publicly accessible data with
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10 541 journal publications e.g. in Dryad (<http://datadryad.org>), sometimes with embargo periods.
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12 542 However, this can be complicated when article authors are not the 'owners' of the data, different
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14 543 legislation applies across countries and states, and the databases themselves continue to evolve;
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17 544 efforts to resolve these and other issues (e.g. the incentive to invest in long-term studies when
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19 545 'scroungers' can get benefits without investing to the extent of 'producers') are ongoing (Mills et
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21 546 al. 2015, Whitlock et al. 2016, Mills et al. 2015). For vegetation resurveys, Wiser (2016) suggests
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23 547 archiving plot data in an established vegetation plot repository as a first step and then providing
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25 548 versioned data to meet journal requirements as a second step, while others suggest summary data
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27 549 be provided to allow reproducible analyses, with primary data only being available after requests
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29 550 to collaborate (Mills et al. 2015). This latter approach is similar to forestREplot, where the data are
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31 551 archived but not publically accessible; instead, requests for new analyses are considered by a
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33 552 Management Committee to avoid overlap with existing projects, and dataset contributors are then
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35 553 contacted to give permission for data use.
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40 554 Care also needs to be taken with the public accessibility of vegetation data, e.g. to avoid explicit
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42 555 location of species of conservation concern. However, arguments exist that we will only get
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44 556 solutions to environmental issues if data are made easily accessible to, and understood by, a
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46 557 broad audience (Peters 2010). Ultimately, records of data existence would be invaluable for
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48 558 researchers, as would instructions for how interested parties can access them with associated
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50 559 rights of use – through for example the distributed system of national and international funded
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52 560 data platforms as proposed by the World Data System of the International Council of Science
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(Bendix et al. 2012). In addition to electronic data, records that need to be kept according to rigorous procedures include field notes, samples, photographs, and maps.

PROCEDURES FOR ROBUST ARCHIVING OF RE-SURVEY RECORDS

- **Depository**
Records to be reliably stored with explicit archiving function
- **Index and Catalogue**
Classmark all items e.g. maps, photograph, digital records
Description of contents preferably using Ecological Metadata Language
- **Institutional Memory**
Ensure knowledge of data existence within institution and more broadly.
Best achieved through online repositories e.g. DataONE.
- **Access and Ownership Arrangements**
Clarify rights, costs and legitimate purposes for record use
Detail ownership of records
- **Additional Material Deposition**
Clear controls and guidelines for additional data deposition

Figure Box 1: Procedures for the robust archiving of resurvey records. Data may not need to be made available to all but it is crucial that its existence not be forgotten given the opportunity they provide to answer fundamental ecological questions. Given the pressure for scientists to publish, archiving may ultimately be best incentivised through credit for data publication. In the meantime, and while barriers to this outcome are still present, it is imperative that metadata and the records themselves are robustly archived with researchers able to find out about their existence through online search tools e.g. DataONE.

Table 1. Overview of criteria used to decide on the inclusion of datasets in multiregion community resurvey studies, illustrated with the decisions taken to feed the ‘forestREplot’ network with datasets.

Dataset inclusion criteria	forestREplot	
	Criteria	Rationale
<i>General criteria</i>		
Suitable for the scientific goals and questions at hand?	Forest ground layer resurveyed at multiple locations within a region with more or less similar site conditions, including climate, major soil types and levels of atmospheric deposition	This type of data structure is needed to isolate the effects of drivers acting at larger scales, such as changing climate or levels of atmospheric pollutant deposition from effects of drivers acting at a more local scale, such as management changes (see also Fig. 1)
<i>Specific criteria</i>		
Relevant geographic region?	Temperate forest as defined by Olsen et al. (2001)	Ground layer in temperate forest comprises the majority of plant diversity and has an important impact on ecosystem functioning
Relevant system characteristics?	Natural and semi-natural forests according to Peterken (1996). Both are composed of locally native trees and shrubs which often derive from natural regeneration or coppicing rather than planting (in case of semi-natural forests) or have not been managed at all (in case of natural forest)	Management actions such as soil working and fertilization may completely override effects of other global change drivers
	Between the two surveys, no human-induced conversion to stand types no longer in line with the natural or semi-natural forest criteria has taken place	
Relevant study design?	(Quasi-)permanent plots	Minimizes so-called pseudo-turnover
	At least 20 plots which can be treated as independent observations (i.e. distributed over a sufficiently large area) per dataset	Sufficient replicates within single regions are needed
	At least 20 years between the oldest and most recent survey	Forest ground layer vegetation often shows delayed responses to environmental changes
	Plot size varies between 1 m ² and 1000 m ²	Plots falling within this size range are expected to present a representative picture of the ground layer vegetation community
Relevant response variables?	Presence/absence or cover data of all vascular plants in the ground layer community	Needed to get a complete view on community change

Table 2. Top ten of the most important ecological questions following Sutherland et al. (2013) that can be addressed with the multi-site ground layer resurvey data incorporated in the forestREplot-database.

Rank	Question [§]	Category [§]	Prob[rank='very suitable'] [*]
1	Can we predict the responses of ecosystems to environmental change based on the traits of species?	Ecosystems and functioning	0.67
2	How do spatial and temporal environmental heterogeneity influence diversity at different scales?	Communities and diversity	0.64
3	What is the magnitude of the extinction debt following the loss and fragmentation of natural habitats, and when will it be paid?	Human impacts and global change	0.58
4	Which ecosystems and what properties are most sensitive to changes in community composition?	Ecosystems and functioning	0.51
5	To what extent is local species composition and diversity controlled by dispersal limitation and the regional species pool?	Communities and diversity	0.50
6	How well can community properties and responses to environmental change be predicted from the distribution of simple synoptic traits, e.g. body size, leaf area?	Communities and diversity	0.48
7	What are the indirect effects of harvesting on ecosystem structure and dynamics?	Human impacts and global change	0.48
8	How do natural communities respond to increased frequencies of extreme weather events predicted under global climate change?	Human impacts and global change	0.40
9	What are the most appropriate baselines for determining the magnitude and direction of ecological changes?	Methods	0.39
10	In the face of rapid environmental change, what determines whether species adapt, shift their ranges or go extinct?	Human impacts and global change	0.37

§: taken from the list of Sutherland et al. (2013)

* We fitted cumulative link models, which are regression models for ordinal data (*clm* in the R package ordinal; Christensen 2015, R Core Team 2015). Results show the estimated probability that a question was rated as 'very suitable' across the 32 respondents.

Table 3. Impact of selected environmental drivers on changes in ground layer species richness in temperate forests. Shown are exemplarily single-region studies and, per environmental driver, its estimated general importance based on multi-region resurvey studies.

Driver	Single-region vegetation resurveys (examples)	Direction of effect on species richness	Multi-region analyses
Increased forest management intensity	Økland et al. (2003) Li and Waller (2015) Kirby and Thomas (2000) Brunet et al. (1996) Decocq et al. (2004) Schmidt (2005) Van Calster et al. (2008) Hédli et al. (2010) Kopecký et al. (2013)	Negative Negative No effect Positive Positive Positive Positive Positive Positive	The most important factor driving understory vegetation composition (Paillet et al. 2010), may mask the effects of climate change (De Frenne et al. 2013), or nutrient deposition (Verheyen et al. 2012)
Increased N-deposition	Hédli (2004) Skrindo and Økland (2002) Bernhardt-Römermann et al. (2007)	Negative No effect Positive	Pre-survey levels of N deposition determine subsequent changes in biodiversity (Bernhardt-Römermann et al. 2015); actual N-deposition is less important than forest management (Verheyen et al. 2012); exceedance of critical loads favors N demanding species (Dirnböck et al. 2014)
Climate warming	Kirby et al. (2005) Heinrichs et al. (2012) Naaf and Wulf (2010, 2011) Savage and Vellend (2015)	Negative No effect Positive Positive	Buffering effects of canopy closure on increased dominance of warm-adapted species as a result of climate warming (De Frenne et al. 2013)

Figure captions

Figure 1. Collecting data across multiple regions will generate insights that cannot be obtained from single-region studies. In this hypothetical example for forests, nevertheless inspired by De Frenne et al. (2013), alpha-diversity losses and gains over time are observed in colder and warmer regions, respectively. The within-region microclimatic variation caused by closing or opening tree canopies between the two surveys respectively attenuates or reinforces this general trend in alpha-diversity change across the macroclimatic gradient. Only sampling a few locations from each region would show a simplistic relationship and likely lead to incorrect inference.

Figure 2. Comprehensiveness, representativeness, and orthogonality of single-region vs. multiple-region resurveys and experiments. Experiments are more orthogonal than observatories. The combination of multiple regions typically creates higher orthogonality and generates more comprehensive and representative results than from a single region. The red arrow indicates that orthogonality and representativeness are not entirely independent in multi-region resurvey observatories: the inclusion of multiple regions is generally a necessary condition to increase orthogonality between drivers of change and this will simultaneously increase the representativeness.

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Figure 1

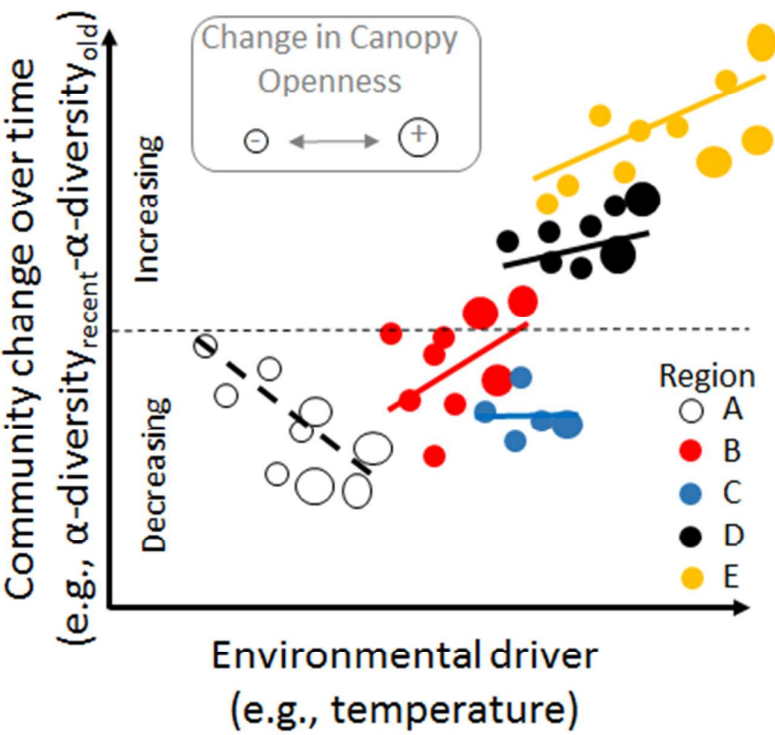


Figure 2

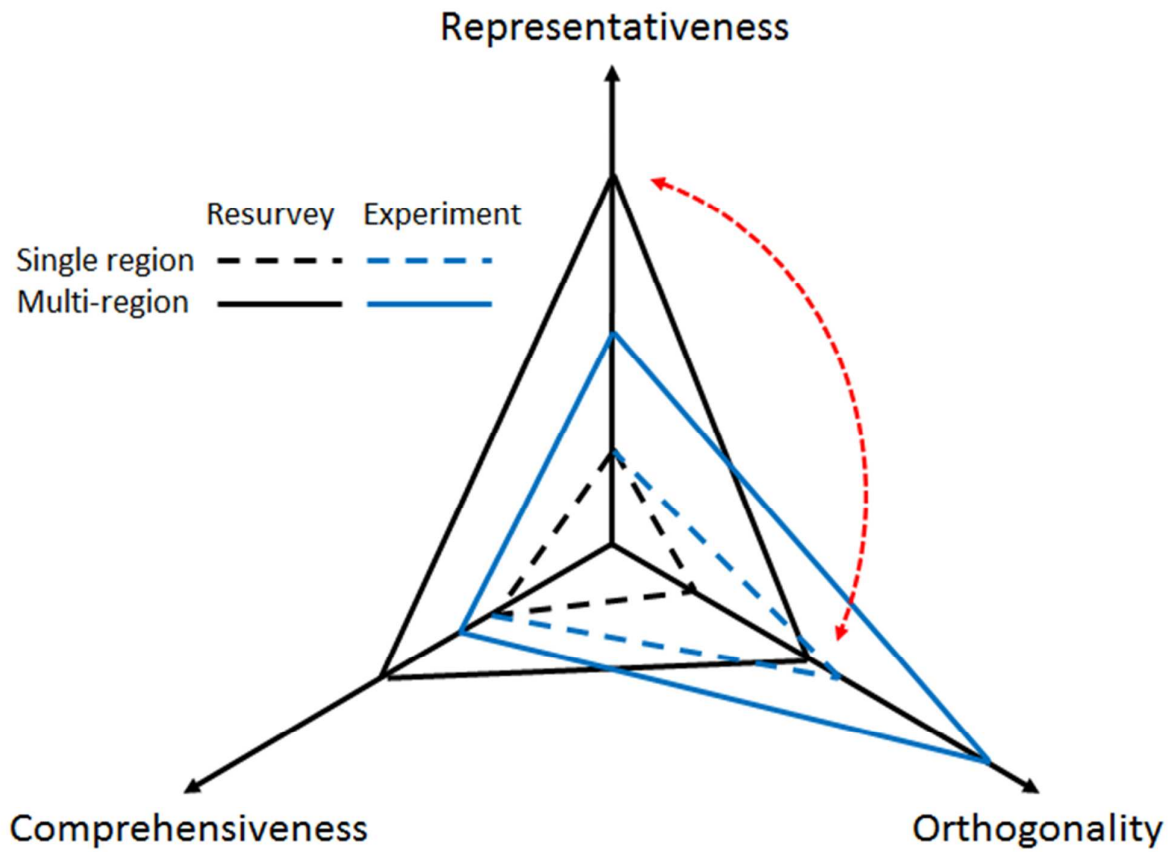


Table S1: Details of the study sites included in forestREplot.

ID	Study region	Continent	Country	Lat	Long	Study area	Plot size (range)	Plot nr.	Survey year(s)	
				°N	°E	ha	m ²		Initial	Recent
1	Zöbelboden	Europe	A	47.8	14.4	90	100-100	18	1993	2005-2010
2	Binnen-Vlaanderen	Europe	B	51.1	3.5	30000	100-200	39	1977-1983	2009
3	Florenne	Europe	B	50.2	4.6	362	100	58	1957	2005
4	Gaume	Europe	B	49.6	5.6	1000	50-400	43	1953-1963	2008
5	Herenbossen	Europe	B	51.1	4.8	45	196	111	1980	2004
6	Meerdaalwoud	Europe	B	50.8	4.7	1319	125-225	21	1954	2000
7	Tournibus	Europe	B	50.3	4.6	228	100	139	1967	2005
8	Vorte Bossen	Europe	B	51.1	3.4	50	150	26	1977-1980	1998
9	Zoerselbos	Europe	B	51.3	4.7	30	100	17	1982	2008
10	Switzerland	Europe	CH	47.3	7.8	1500000	100-400	37	1940-1965	1998
11	České středohoří	Europe	CZ	50.6	14.1	8700	500	95	1965	2012
12	Děvín Wood	Europe	CZ	48.9	16.6	350	100-1300	50	1953-1963	2002
13	Hodonínská Důbrava	Europe	CZ	48.9	17.1	3600	400	55	1965	2012
14	Krumlov Wood	Europe	CZ	49.1	16.4	3300	400	60	1964-1968	2012
15	Miličovský les	Europe	CZ	50	14.5	93	50-625	19	1986	2008
16	Milovice Wood	Europe	CZ	48.8	16.7	2100	500	46	1953	2006
17	Rychlebské hory Mts.	Europe	CZ	50.3	17.1	4800	315	21	1941-1943	1998-1999
18	Ždánice Wood	Europe	CZ	49.1	17	15000	500	121	1959-1963	2012
19	Brandenburg	Europe	D	52.1	13.9	295	100-400	126	1963-1965	2012
20	EchingerLohe	Europe	D	48.3	11.7	24	100	125	1986	2003
21	Elbe-Weser	Europe	D	53.6	9	750000	100-400	50	1986-1989	2008
22	Göttingen, Carici-Fag.	Europe	D	51.3	9.8	4000	30-400	78	1955-1960	2011-2012
23	Göttingen, Hordelymo-Fag.	Europe	D	51.6	10	4000	75-400	35	1955-1967	2009
24	Göttingen, Hünstollen	Europe	D	51.6	10	56	100-250	147	1992	2012
25	Göttingen, SFB	Europe	D	51.5	10.1	12	100-400	42	1980	2001
26	Prignitz	Europe	D	53.1	12.3	282340	400	119	1954-1960	2014
27	Andigny	Europe	F	50	3.6	> 3000	500-800	19	1957-1963	1995-1996
28	Hirson	Europe	F	49.9	4.1	> 1000	500-800	22	1956-1965	1996-1999

Table S1: Continued.

ID	Study region	Country	Lat	Long	Study area	Plot size (range)		Plot nr.	Survey year(s)	
						ha	m ²		Initial	Recent
29	Jura	Europe	F/ CH	46.8	6.4	2268600	200-400	164	1989	2007
30	Wytham Woods	Europe	GB	51.8	-1.3	340	100	71	1974	1999
31	Heves	Europe	H	48	20.5	5.5	625	10	1989	2008
32	Nyírség	Europe	H	47.3	22.3	50	25	11	1930-1936	1990
33	Killarney National Park	Europe	IRL	52	-9.5	350	8	16	1991	2011
34	Speulderbos	Europe	NL	52.3	5.7	1000	100-250	27	1957-1959	1987-1988
35	Hordaland	Europe	NO	6.1	60.3	8376	25	40	1978-1980	2007-2009
36	Bazaltowa Mt	Europe	PL	51	16.1	110	200	21	1992-1994	2010-2014
37	Białowieża	Europe	PL	52.7	23.9	4747	100-200	22	1966	2012
38	Buki Sudeckie beech forest	Europe	PL	50.9	16	174	100-160	16	1990	2014
39	Sanocko-Turczańskie Mts	Europe	PL	49.5	22.3	25000	100-400	71	1972-1973	2005-2007
40	Trzebnickie Hills	Europe	PL	51.3	16.8	9 and 16	200	20	1962	2011
41	Dalby	Europe	S	55.7	13.3	36	1 (16 canopy)	74	1935	2010
42	Öland	Europe	S	56.4	16.4	100000	225	51	1988	2014
43	Skåne	Europe	S	55.9	13.7	500	500	70	1983	2014
44	Stenshuvud	Europe	S	55.7	14.3	0.08	5	30	1988	2008
45	Tullgarn	Europe	S	59	17.6	14.5	100	127	1971	2003
46	Slovakia, Central	Europe	SK	48.3	19.4	70000	500	21	1964-1973	2005-2007
47	Slovakia, North-East	Europe	SK	49.2	21.9	40000	500	22	1965-1974	2006
48	Slovakia, South-West	Europe	SK	48.4	17.3	25000	500	18	1966-1972	2007
49	Lady Park	Europe	UK	51.7	-2.7	35	32	35	1979	2009
50	Mont Mégantic	N-America	CAN	45.5	-71.2	5490	400-800	48	1970	2012
51	Central Wisc. sand plains	N-America	US	44.2	-90.5	885800	20-50	30	1958	2012
52	Dukes	N-America	US	46	-87.2	100	1	74	1978-1980	2002-2007
53	Fernow Exp. Forest, WV	N-America	US	39.1	-79.8	70	10	14	1991	2003
54	Great Smoky Mountains	N-America	US	35.5	-83.8	13100	1000	18	1977-1978	1995
55	Northern Wisconsin	N-America	US	46.8	-91	1500000	20	66	1949-1950	2000

Appendix II

Table All-1 Subset of 42 fundamental questions in ecology (as listed by Sutherland et al., 2013) that were retained after the workshop organizers performed a pre-screening for their suitability to be answered by using the forestREplot-database. The 42 questions are ranked by the potential of the forestREplot-database to address each question, according to the scoring of all workshop participants.

Rank	Question §	Category §	Prob [rank='very suitable']*
1	Can we predict the responses of ecosystems to environmental change based on the traits of species?	Ecosystems and functioning	0.67
2	How do spatial and temporal environmental heterogeneity influence diversity at different scales?	Communities and diversity	0.64
3	What is the magnitude of the extinction debt following the loss and fragmentation of natural habitats, and when will it be paid?	Human impacts and global change	0.58
4	Which ecosystems and what properties are most sensitive to changes in community composition?	Ecosystems and functioning	0.51
5	To what extent is local species composition and diversity controlled by dispersal limitation and the regional species pool?	Communities and diversity	0.50
6	How well can community properties and responses to environmental change be predicted from the distribution of simple synoptic traits, e.g. body size, leaf area?	Communities and diversity	0.48
7	What are the indirect effects of harvesting on ecosystem structure and dynamics?	Human impacts and global change	0.48
8	How do natural communities respond to increased frequencies of extreme weather events predicted under global climate change?	Human impacts and global change	0.40
9	What are the most appropriate baselines for determining the magnitude and direction of ecological changes?	Methods	0.39
10	In the face of rapid environmental change, what determines whether species adapt, shift their ranges or go extinct?	Human impacts and global change	0.37
11	What is the relative importance of stochastic vs. deterministic processes in controlling diversity and composition of communities, and how does this vary across ecosystem types?	Communities and diversity	0.36
12	What determines the rate at which species distributions respond to climate change?	Human impacts and global change	0.36
13	How successful have past ecological predictions been and why?	Methods	0.36
14	To what extent is biotic invasion and native species loss creating ecosystems with altered properties?	Ecosystems and functioning	0.31
15	How important are dynamical extinction-recolonization equilibria to the persistence of species assemblages in fragmented landscapes?	Communities and diversity	0.29

16	How relevant are assembly rules in a world of biological invasion?	Communities and diversity	0.29
17	How do we combine multiple scales and types of monitoring (from field to earth observation) to make robust ecological inferences?	Methods	0.29
18	What demographic traits determine the resilience of natural populations to disturbance and perturbation?	Populations	0.27
19	Under what circumstances do landscape structures such as corridors and stepping stones play important roles in the distribution and abundance of species?	Human impacts and global change	0.25
20	Which, if any, species are functionally redundant in the context of stochastic or directional environmental changes?	Ecosystems and functioning	0.25
21	How does species loss affect the extinction risk of the remaining species?	Communities and diversity	0.25
22	How is ecosystem function altered under realistic scenarios of biodiversity change?	Ecosystems and functioning	0.22
23	How do species and population traits and landscape configuration interact to determine realized dispersal distances?	Populations	0.21
24	What are the contributions of biogeographical factors and evolutionary history in determining present day ecological processes?	Communities and diversity	0.21
25	How do interspecific interactions affect species responses to global change?	Human impacts and global change	0.21
26	Which factors and mechanisms determine the resilience of ecosystems to external perturbations and how do we measure resilience?	Ecosystems and functioning	0.20
27	Do different demographic rates vary predictably over different spatial scales, and how do they then combine to influence spatio-temporal population dynamics?	Populations	0.19
28	How does environmental stochasticity and environmental change interact with density dependence to generate population dynamics and species distributions?	Populations	0.19
29	How can we tell when an ecosystem is near a tipping point?	Ecosystems and functioning	0.16
30	Which mechanisms allow the long-term coexistence of grasses and woody plants over a wide range of ecosystems?	Communities and diversity	0.14
31	What are the evolutionary and ecological mechanisms that govern species' range margins?	Populations	0.13
32	How important are rare species in the functioning of ecological communities?	Communities and diversity	0.13
33	Which ecosystems are susceptible to showing tipping points and	Ecosystems and	0.13

	why?	functioning	
34	What is the relative contribution of biodiversity at different levels of organization (genes, species richness, species identity, functional identity, functional diversity) to ecosystem functioning?	Ecosystems and functioning	0.13
35	How do we best develop and exploit empirical model systems for understanding natural systems?	Methods	0.13
36	How do we predict mechanistically how many species can coexist in a given area?	Communities and diversity	0.11
37	Is hysteresis the exception or the norm in ecological systems?	Ecosystems and functioning	0.11
38	How will atmospheric change affect primary production of terrestrial ecosystems?	Human impacts and global change	0.11
39	What are the major feedbacks and interactions between the Earth's ecosystems and the atmosphere under a changing climate?	Human impacts and global change	0.11
40	How do species traits influence ecological network structure?	Communities and diversity	0.10
41	How do resource pulses affect resource use and interactions between organisms?	Communities and diversity	0.09
42	What are the evolutionary consequences of species becoming less connected through fragmentation or more connected through globalization?	Evolution and ecology	0.06

§: taken from the list of Sutherland et al. (2013)

* We fitted cumulative link models, which are regression models for ordinal data (*clm* in the R package ordinal; Christensen 2015, R core team 2015). Results show the estimated probability that a question was rated as ‘very suitable’ across the 32 respondents.