

Why we *still* need permanent plots for vegetation science

1 | INTRODUCTION

The use of permanent plots has a long tradition in ecology (Callahan, 1984; Wildi and Schültz, 2000; Lindenmayer *et al.*, 2012; Hughes *et al.*, 2017) and vegetation science (Bakker *et al.*, 1996a). Recently, permanent-plot studies were considered among the six most important developments in vegetation science (Chytrý *et al.*, 2019). As the present Special Feature demonstrates, the value of permanent plots is becoming ever more evident as a growing number of available time series highlights the variability inherent in plant communities and the non-linear ways in which community composition and function respond to global change. In a previous Special Feature in *Journal of Vegetation Science* edited by Bakker *et al.* (1996a), different contributors showed the importance of permanent plots in understanding the mechanisms underlying vegetation changes, particularly following succession. Bakker *et al.* (1996a) used the term 'permanent plots' broadly to 'include studies in which a series of randomly located plots or transects have been described at certain time intervals within a fixed area'. Such permanent plots are thus based on regular observation of the temporal dynamics of vegetation using sampling units with a fixed location in time, while the sampling approach is kept consistent.

A similar approach is the resurvey of vegetation plots. The topic of vegetation resurvey was well covered recently in a stimulating Special Feature in the sister journal *Applied Vegetation Science* (Hédl *et al.*, 2017). In this approach, historical vegetation plots (usually older than two decades) are resampled using the same or similar sampling method, though not always using the same exact geographical location (Alstad *et al.*, 2016). Vegetation resurveys are often conducted when contemporary researchers wish to capture trends in vegetation response to environmental changes – such as climate change – that the original researchers did not anticipate (Harrison *et al.*, 2010). These opportunistic studies aim to make the best use of existing data and allow earlier observations than many permanent-plot studies, but a downside of this approach is the potential risk of relocation and sampling biases (Kapfer *et al.*, 2017). The distinction between permanent plots and semi-permanent (or quasi-permanent) plots used in the vegetation resurvey approach is often not definite, and both approaches can be very useful to assess medium- to long-term trends in vegetation (Figure 1). At the same time, as further discussed in this Special Feature, frequent and regular sampling using permanent plots allows the assessment

of species dynamics and community stability (Figure 1 and Special Feature) in addition to longer-term trends. Within permanent plots, we can further differentiate between observational plots and experimental plots, where natural or semi-natural vegetation is sampled after the application of experimental treatments in the latter. The difference between these types of plots is that experimental set-ups are affected by both experimental treatments and natural variability. Establishing and, when needed, maintaining the treatments can require additional effort.

Sampling with a long-term view takes effort. As summarized by Bakker *et al.* (1996a) 'it needs a great deal of discipline to maintain a series of permanent plots and analyse them yearly over a period long enough to answer relevant (ecological) questions'. The commitment of individual researchers to permanent-plot sampling have significantly advanced the field of ecology. For example, permanent-plot studies spearheaded by a few individuals have elucidated the cyclical nature of population dynamics (The Portal Project; Morgan Ernest *et al.*, 2016), and the role of disturbance for diversity (Jasper Ridge; Hobbs *et al.*, 2007). Such discipline, however essential, is likely not the only trait required of researchers who successfully undertake the challenge of establishing and maintaining permanent plots for many years. Researchers also need to be able to secure support from institutions, either academic or governmental, including continuous funding, special agreement with landowners, security at the sampling sites and safe and stable data storage. Institutional support is likely a major bottleneck, particularly in the context of predominantly short-term scientific support from most existing grant agencies. Because of this, most field observations and experiments are conducted only over short periods, despite the fact that environmental drivers work over long time periods, the response of vegetation could be delayed in time (see extinction debt; Helm *et al.*, 2006) and that the effect of management may have long-term legacies (e.g., short-term fertilization effects detectable after 70 years; Spiegelberger *et al.*, 2006). With some notable exceptions (e.g., Crawley *et al.*, 2005; Silvertown *et al.*, 2006), many permanent-plot sampling schemes do not exceed a few decades, often overlapping with the career of a few dedicated researchers. Developing funding mechanisms to support the long-term work of individual research teams provides the missing support needed.

A limited number of national and international initiatives have successfully launched and maintained permanent vegetation monitoring schemes worldwide, particularly using forest and grassland

plots. For example, the Center for Tropical Forest Science established a global network of forest inventory plots in the 1980s (Anderson-Teixeira *et al.*, 2015). Currently, together with standardized sampling and data storage (Condit *et al.*, 2014), this evolved into the ForestGEO initiative (<https://forestgeo.si.edu/what-forestgeo>). Similar initiatives include, for example, the Chinese Forest Biodiversity Monitoring Network (<http://www.cfbiodiv.org/>; De Cáceres *et al.*, 2012), the Brazilian Biodiversity Research Program (Magnusson *et al.*, 2018), the Spanish Forest Inventory (Ruiz-Benito *et al.*, 2013) or New Zealand's Land Use and Carbon Analysis System (Holdaway *et al.*, 2017). In 1980, the US National Science Foundation established the Long-term Ecological Research (LTER) program, which supports a network of 28 sites to offer a long-term view on ecological dynamics. Today, research programmes at multiple LTER sites (including in other regions of the world), provide open-access ecological data to answer a number of pressing ecological questions across taxa. Other national initiatives, such as the Biodiversity Exploratories (BE), a German Science Foundation-funded project, maintain a very exhaustive standardized sampling of plots along a land-use intensity gradient in different regions. Similarly, the Environmental Change Network (ECN) focuses on monitoring, data and research to understand environmental change in the United Kingdom. Some initiatives have established a common sampling scheme to follow trends in composition and diversity in specific ecosystems, such as mountain summits (e.g., Pauli *et al.*, 2012) or tundra (Elmendorf *et al.*, 2012), although these sites are not always sampled on an annual basis.

Establishing comparable sampling schemes in different regions and habitats represents an ideal solution to develop robust monitoring schemes. However, this clearly requires a highly coordinated effort, with common and stable funds, which unfortunately is still often unrealistic. Moreover, there is a balance between standardized, comparable designs across systems and long-term experiments

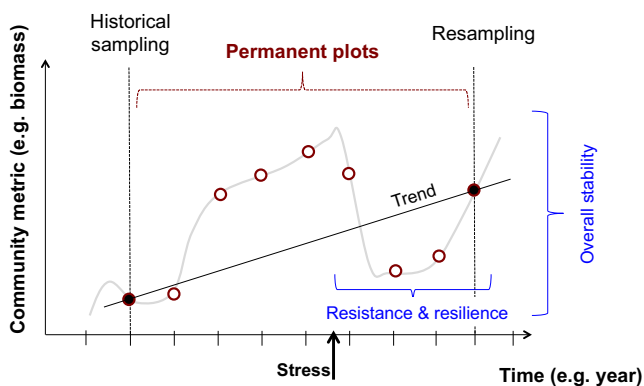


FIGURE 1 A schematic representation of the variation of permanent plot data and their use to answer questions related to temporal trends and components of ecological stability (including resistance and resilience after stress and exceptional weather conditions). The overall stability is the result of the interplay between variations in environmental conditions and biotic interactions. Notice that, in practice, permanent plots usually cover shorter time intervals than resurveys of historical plots

tailored to test key purported dynamics of an individual system, with their specificities. Initiatives such as the ones mentioned above are restricted either to a few countries or to particular habitats and organisms. However, a number of 'grassroot' initiatives (Aubin *et al.*, 2020) have developed worldwide to implement distributed, replicated permanent-plot experiments (e.g., the global Nutrient Network, NutNet, <https://nutnet.org/>, Borer *et al.*, 2014, or DroughtNet, <https://drought-net.colostate.edu/>). At the same time, synthesis efforts have developed to compile permanent-plot data, irrespective of specific sampling methods, across individual studies for cross-site comparisons. For example, BioTIME (Dornelas *et al.*, 2018) is an impressive initiative that collects data from existing long-term sampling schemes for different organisms from independent sources for a minimum of two years, although not necessarily consecutively. This type of data, despite the sampling differences, can be effective to assess large-scale trends in biodiversity (Dornelas *et al.*, 2014; Blowes *et al.*, 2019).

A particularly interesting example of independent efforts to monitor biodiversity in time is the Park Grass Experiment (e.g., Crawley *et al.*, 2005; Silvertown *et al.*, 2006). The Park Grass Experiment, begun in 1856, is likely the oldest ongoing ecological experiment. Its value to science has changed and grown since it was established to test primarily agricultural questions. Particularly in recent years, the interest in the original experiment has transcended its initial aim and facilitated tests of questions related to the mechanisms governing the relationship between biodiversity and productivity and the response of plant communities to atmospheric nutrient deposition (Storkey *et al.*, 2016). Hence, the Park Grass initiative illustrates how long-term experiments grow in value with time and how they may be used to investigate scientific questions that were inconceivable at their inception.

The papers in this Special Feature cover a number of long-term studies that show how permanent plots can be essential to answering a number of important ecological questions. Some papers focus on the unique characteristics of individual sites (Brambila *et al.*, 2020; Burge *et al.*, 2020; Collins *et al.*, 2020; Fischer *et al.*, 2020; Herben *et al.*, 2020) or intensive long-term experimental manipulations (Hédli and Chudomelová, 2020; Liu *et al.*, 2020; Rychtecká and Lepš, 2020; Ward *et al.*, 2020) to test long-standing ecological theories. Others combine long-term data sets to identify general patterns across biomes, e.g., Ward *et al.* (2020), or Valencia *et al.* (2020, with the LOng-Term Vegetation Sampling, LOTVS).

The pressing threat from multiple global change drivers and the need to follow their consequences in different regions and habitats worldwide call for coordinated efforts using repeated monitoring tools such as permanent plots (Borer *et al.*, 2014). For this reason, we think it is important to answer the question: why do we *still* need to invest time, effort and funding in permanent plots? Following Bakker *et al.* (1996b), this Special Feature is an attempt to provide answers to this question and illustrate the need for special funding schemes beyond conventional ones that are based on short-term funding cycles.

2 | PERMANENT PLOTS AS A TOOL FOR VEGETATION SCIENCE

The title of this section is inspired by Herben's contribution (1996) in the Special Feature edited by Bakker *et al.* (1996a). Here we explore different ways in which permanent plots can be employed as a tool to answer a variety of pressing ecological questions. We can broadly classify these questions into two very general, and inter-related, groups: (a) mechanisms causing and maintaining biodiversity; and (b) long-term vegetation dynamics under historical as well as novel environmental drivers and their consequences for ecosystem functions. We illustrate some key examples from the literature for both of these questions and their interactions. We then show how the collection of studies in this Special Feature advances our understanding of both sets of questions and provides perspectives for future ecological research.

Assessing the spatial and temporal scales of species turnover in permanent plots has been repeatedly identified as key to understanding the mechanisms maintaining species diversity (Herben, 1996). In 1993, van der Maarel and Sykes (1993) formulated the so-called 'carousel model' based on some earlier ideas by Herben *et al.* (1993), i.e., high temporal mobility of species in relatively homogeneous habitat conditions supporting a temporal turnaround of species as a mechanism of maintenance of biodiversity. This finding is consistent with the studies of Sale (1978) and Chesson and Warner (1981) on lottery systems in high-diversity coral reefs, with a rapid turnover with little or no niche differentiation. They are also consistent with the findings of negative plant–soil feedbacks (Chung *et al.*, 2019). More recent studies (Rychtecká and Lepš, 2020, this issue) have shown a pronounced difference in mobility among species, from typical stable 'sitters' to more mobile 'travellers', in species-diverse wet-meadow communities. The results of Rychtecká and Lepš can also be interpreted in terms of species traits, which are becoming an essential tool for ecologists (Pillay and Ward, 2014; Giarrizzo *et al.*, 2017). Also, they reported greater mobility for species with more 'acquisitive' strategies (high specific leaf area [SLA], high nitrogen leaf content) and species with well-developed clonal organs of lateral spread. Interestingly, in the same communities, species also differentiated into different types of temporal fluctuation (with more or less stable populations in time; Májeková *et al.*, 2014), although such differentiation was not correlated with differences in species' spatial stability. These types of studies using data from permanent plots provide an exciting venue to understand how the complex interaction between spatial and temporal fluctuations can allow for regeneration niches of different species, and how local diversity is maintained.

Permanent plots can be further used to directly extract essential and unique information about species interactions (Damgaard *et al.*, 2009; Adler *et al.*, 2012; Tredennick *et al.*, 2017; Garnier *et al.*, 2018; Herben *et al.*, 2019). This makes possible the separation of mechanistic/deterministic components of community dynamics from environmental and demographic stochasticity, as well as parameterizing a mechanistic model of community functioning that can be used

for further predictions under different scenarios (Adler *et al.*, 2012; Tredennick *et al.*, 2017). In another study in this Special Feature, located in a mountain meadow, spatially explicit ramet counts of 20 coexisting species were collected (very patiently) at a scale of 3 cm × 3 cm grid cells (Herben *et al.*, 2020, this issue). Bayesian models showed large variation in pairwise species competition coefficients behind species' temporal and spatial fluctuations. By considering species traits in combination with spatial and temporal fluctuations, it was possible to provide a novel insight into species coexistence. While competition was generally found to be size-asymmetrical, with bigger species over-competing smaller ones, trait differences contributed to within-community niche differentiation. This was likely done by reducing competition between co-occurring grassland species, with a potential role in species coexistence.

While these studies demonstrate high species mobility at very fine spatial scales, at coarser spatial scales (i.e., bigger plot sizes), we expect lower floristic variation, often without any trend in composition. This idea was initially proposed by both van der Maarel and Sykes (1993) and Herben *et al.* (1993), as also demonstrated subsequently by Wilcox *et al.* (2017). In this issue, Fischer *et al.* (2020) observed remarkable year-to-year dynamics within plots in a dry grassland site, with plant responses to weather patterns over the previous two years. These community changes were found to be non-directional and contributed to the stability of this grassland, which has changed little over the past 90 years, consistently with the expectations of van der Maarel and Sykes (1993). In fact, the presence of species with different responses to environmental conditions within a community is a key mechanism promoting overall temporal stability of communities, i.e., compensatory dynamics (McCann, 2000) – see also below and Valencia *et al.* (2020, this issue). Fischer *et al.* stress, however, that increasing frequency of drought events due to ongoing climate change could eventually result in disrupting such long-term stability and cause a directional change, such as an increased number of ruderal species and their higher population density. Only continued monitoring of these permanent plots will make it possible to test this hypothesis.

Ongoing environmental changes can indeed drive directional trends in species composition. Ecosystems respond to chronic environmental changes (e.g., elevated CO₂, increased temperature, N deposition) through a series of processes, starting with phenotypic plasticity of individuals on short time scales, followed by a re-ordering of species' abundances at intermediate time scales, and finally by species turnover via colonization and local extinction (Siefert, 2012). Given the delay in changes in vegetation composition, for example via extinction debt (Tilman *et al.*, 1994; Helm *et al.*, 2006), such turnover and directional changes can take several years to occur. Collins *et al.* (2020, this issue), using 400-m permanently located line transects across different community types, showed community re-ordering and composition changes following climatic and disturbance events (caused by fire in their study). They provide a unique perspective on the directionality of vegetation changes, which would be virtually impossible to obtain by using short-term research. Indeed, shorter or less frequent sampling would clearly fail to detect the

complex interplay of periodic climatic events and pulse disturbance through fire.

Without disturbance and under a 'stable' climate, the year-to-year variation could be small, as originally predicted by van der Maarel and Sykes (1993) and shown by Hédél and Chudomelová (2020, this issue) in an eLTER (LTER Europe) site. The interannual turnover detected by monitoring in permanent plots was lower than the long-term changes detected by a resurvey of semi-permanent plots, which showed larger temporal heterogeneity due to the active management at the time of the baseline survey. Coppicing abandonment seven decades ago was followed by a long-term biodiversity decline due to canopy closure (Kopecký *et al.*, 2013). Hédél and Chudomelová also show seasonal variation exceeding the magnitude of interannual changes, indicating the sampling date as a potentially significant source of error. The monitoring designs clearly need to take into account several temporal scales when comparing vegetation dynamics.

Disturbance, for example by herbivores, can both increase and decrease biodiversity (Cingolani *et al.*, 2005), although often these effects are assessed over short temporal scales and on local biodiversity only (alpha diversity). Overall, herbivory can further enhance or dampen the effect of environmental variation on diversity through time. At the Carrizo Plain in California, kangaroo rats engineer a pattern of higher-resource mounds and lower-resource interstitial spaces, which, combined with high rainfall variability, creates a highly spatiotemporally variable landscape. In this environment, Brambila *et al.* (2020, this issue) found that the effect of cattle grazing was highly variable. In high-resource locations under high-resource years, cattle grazing caused biomass and diversity to diverge considerably from ungrazed areas, but at other times the effect of grazing was relatively weak. In line with the results of Collins *et al.* (2020) and Hédél and Chudomelová (2020, both in this issue), the findings of Brambila *et al.* suggest that the extent of species fluctuations in response to disturbance will be moderated by annual weather conditions. It is thus possible that the importance of disturbance events could be missed in short-term studies that did not assess effects within the context of longer-term climate variability.

The study of succession, which motivated the special issue of Bakker *et al.* (1996a), has advanced incredibly, thanks to the repeated sampling of permanent vegetation plots over time. Even so, it is often difficult to determine whether the rate of succession has merely slowed down or reached a steady-state endpoint. Moreover, during succession, taxonomic and functional convergence in communities – that is, when they become more similar with time – should occur if environmental conditions are similar (Pickett *et al.*, 2008). However, convergence is less likely if there is high stochasticity in the species composition of initial recruits, or where the environment is highly heterogeneous. In such circumstances, functional convergence is more likely than taxonomic convergence (Fukami *et al.*, 2005). Due to the general absence of historical long-term sampling spanning more than a few decades, Burge *et al.* (2020, this issue) show that long-term permanent plots, together with pollen and

charcoal reconstructions from cores taken within these permanent plots, have the potential to extend the assessment of vegetation dynamics and to examine and compare ecosystem resilience in the face of changing environmental and climatic stressors. Burge *et al.* thus modernized a historical method of data collection to remeasure one of the longest studies of secondary succession in the world, 128 years after a fire in low-productivity subalpine ecosystems poorly adapted to fire. They showed that directional vegetation changes are still occurring, although they are beginning to approach a steady state. However, both taxonomic and functional convergences are not yet maximized, suggesting that even after a long time, the system is poorly adapted to fire. These results, in the light of different scenarios of climatic changes, and consequent changes in fire regimes, could point to the restructuring of vegetation steady-state conditions.

Successional status and habitat context can also moderate the response of vegetation to increasing drought conditions and extreme episodes of heatwaves. These effects can potentially trigger profound impacts on plant communities, in terms of decreased plant photosynthesis, stem growth and productivity (Liu *et al.*, 2015; Anderegg *et al.*, 2018). Using an experimental approach on natural communities, Liu *et al.* (2020, this issue) assessed the impacts of long-term experimental droughts (ca. –30% rainfall) on Mediterranean shrublands. They found that habitat context (historical climate change, soil depth and successional status) affected the magnitude of climate impacts with synergistic effects of experimental drought and extremely dry years. Again, a deeper understanding of the effect of climate change on vegetation can be made possible only by dedicated sampling repeated over time. Research like that conducted by Liu *et al.* is warranted to explore the changes of simultaneous multiple functions under long-term processes and extremes to enable policymakers to design and implement strategies for the maintenance of sustainable ecosystem biodiversity and functioning under climate change.

If long-term experiments like the Park Grass (see above) or the Rengen Grassland Experiment (Hejzman *et al.*, 2007; Titěra *et al.*, 2020) are rare, even rarer is the possibility to compare the consistency of results, using comparable set-ups, across different regions of the world. Ward *et al.* (2020, this issue) took advantage of comparable experimental designs to test whether vegetation response to grazing, burning and fertilization in a subtropical South African grassland was consistent with corresponding results from the temperate grasslands in the Park Grass Experiment (UK) and Konza Prairie (USA), which is another LTER site (Collins *et al.*, 1998). Despite some relatively minor differences, the authors reported rather consistent vegetation responses across regions, regardless of different climatic conditions and different species pools, which holds promise for generalizations of common community-assembly mechanisms. Similar long-term experiments, such as the Nutrient Network grassland experiments (Borer *et al.*, 2014), which boast over 140 sites across different regions, should be employed for the generalization of ecological predictions over the effect of land use and climatic drivers.

With the lack of broad and comparable initiatives to assess the temporal dynamics of vegetation across different regions of the

world, as mentioned above, it is still possible to collate and analyse data collected from individual initiatives. Using a newly assembled LOTVS dataset comprising a global collection of 77 temporal plant-community datasets, with almost 7,800 individual plots sampled over at least six years, Valencia *et al.* (2020, this issue) disentangle drivers of temporal vegetation stability due to directional trends and year-to-year fluctuations. By using a novel method (Lepš *et al.*, 2019), they analyse common measures of species' temporal synchrony to understand compensatory mechanisms between species (McCann, 2000). As suggested by Fischer *et al.* (2020) and Herben *et al.* (2020, both in this issue), different species' fluctuations (low synchrony) in time could result from either different responses to environmental fluctuations or from changes in competitive hierarchy. Lower synchrony between species is expected to lead to higher community stability based on inter-annual fluctuations. However, a generally neglected problem is that synchrony indices can also reflect the effect of long-term trends (e.g., Collins *et al.*, 2020; Hédal and Chudomelová, 2020; Liu *et al.*, 2020, all this issue), which potentially confuses effects in their interpretation of year-to-year synchrony (see also Ward *et al.*, 2020, this issue, where the purported controls also changed dramatically over the 70 years of their observation). Valencia *et al.* showed the importance of directional trends, particularly following long-term environmental manipulations, which should be disentangled from year-to-year changes due to environmental fluctuations. Given that most pre-existing studies on compensatory dynamics are done under often manipulative conditions, earlier studies on plant community stability might have partially overemphasized the role of compensatory dynamics in real-world ecosystems. In the future, similarly to Fischer *et al.* (2020) and Valencia *et al.* (2020; both this issue) it will thus be important to decompose the effect of fluctuations due to directional trends in vegetation from the effect of year-to-year fluctuations.

3 | CONCLUSIONS

A number of courageous and disciplined ecologists have understood the need to launch and maintain long-term research sites in different types of natural and semi-natural environments to answer a rich range of pressing ecological questions, and also provide data to answer questions that were not conceivable at the time of initiation. Several existing projects are formally included under the umbrella of LTER sites worldwide, resulting in data often available within searching portals such as DEISM-SDR (Wohner *et al.*, 2019) or the Environmental Data Initiative (EDI, <https://environmentaldatainitiative.org/edi/>). Indeed, these initiatives, particularly if sufficiently supported by both academic and governmental institutions, will prove essential to answer both theoretical and applied ecological questions in relation to different global-change scenarios. To increase the potential for comparison across studies, though, common initiatives with comparable sampling schemes can be favoured. The collection of studies presented in this Special Feature embodies the output of many hours of dedicated field sampling and shows different





directions and potential applications in the use of long-term sampling schemes using permanent plots. Indeed, we still need many efforts in the near and far future to maintain existing sites and inspire more ecologists to invest their energies in these rewarding sampling approaches.

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