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Using Yearly-Resolved Time Series to Disentangle Interannual Variability, Directional Change, and Pseudoturnover in Plant Community Composition

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ABSTRACT

Questions: Change in species composition over time is the result of both interannual variability, that is, year-to-year fluctuations due to weather patterns or demographic processes, and directional change, following succession or changing climatic conditions. Quantifying each component is difficult due to the confounding effects of pseudoturnover (i.e., apparent turnover due to observer error). Can yearly-resolved vegetation plot time series be used to quantify the relative contribution of these components of change, while controlling for pseudoturnover?

Location: A European beech (*Fagus sylvatica*) forest in Central Apennines, Italy.

Methods: We developed an approach based on matrix decomposition and PERMANOVA to disentangle the effect of pseudoturnover, directional change, and interannual variability across nine permanent vegetation plots resurveyed for thirteen consecutive years, comparing the herb layer in a newly formed canopy gap, at the gap margins, and in the forest interior. We used helical graphs, generalized linear models, and non-metric multidimensional scaling to compare the timing and pace of vegetation change.

Results: Interannual variability and directional change accounted for similar shares of overall variation (26.7% and 28.9%, respectively). While pseudoturnover accounted for a modest 0.4%, ignoring it would result in a substantial overestimation of interannual variability. Overall, the herb layer reacted vigorously to disturbance-triggered changes in light conditions. Species richness increased from 11 to 23.3 in canopy gaps but remained stable at the gap margin and in the forest interior. The rate of change was 3.0 species/year immediately after disturbance and slowed down to 0.3 species/year after 11 years.

Conclusions: The composition of the herb layer varied substantially in the study period and showed a marked year-to-year variation even in the forest interior, where light conditions were relatively stable. A proper estimation of the interannual variability of vegetation, while crucial to benchmark the effects of disturbance in forests, should account for the confounding effect of pseudoturnover.

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1 | Introduction

Accurately monitoring forest biodiversity over time is crucial to assess the effects of climate change and to ensure that forests keep supporting many key ecosystem services and sequestering carbon (Ferretti and Chiarucci 2003; Gilliam et al. 2016; Knollová et al. 2024). Yet, monitoring biodiversity is a challenging endeavor in these slow-responding systems due to the mismatch between the time horizons of forest dynamics (decades to centuries) and human ability to observe them (years to decades) (Hédl and Chudomelová 2020).

The temporal dynamics of forests, like other ecosystems, have many interrelated aspects, which span across multiple temporal scales (Bakker et al. 1996; Pickett et al. 2013). At short temporal scales (e.g., from year to year), forest communities vary as the result of demographic processes of mortality and recruitment, weather patterns, and stochastic events of colonization or local extinction (Chaideftou et al. 2012). When environmental conditions are relatively stable, this year-to-year variability in species composition represents the baseline change rate of the systems. When environmental conditions do change, forests might undergo a directional transformation in composition and structure due to successional processes that are visible only at longer temporal scales (years to decades) (Lepš et al. 2019). These successional dynamics can follow a disturbance event or represent the community response to forest aging or to the slow shift of environmental conditions, such as changing rates of N deposition or climate change (Kermavnar and Kutnar 2024). Detecting the directional component of change is the goal of most monitoring programs, which justifies the recent surge in interest in resurvey studies (Jandt et al. 2022; Sabatini et al. 2023; Knollová et al. 2024). However, it remains theoretically and empirically challenging to distinguish between baseline and directional change in long-term datasets, especially in a context of ongoing global change where environmental conditions are no longer stationary. While climate has always fluctuated, the concept of baseline change extends beyond climate alone and applies to any driver of ecological transformation—including land use, nutrient deposition, or natural succession. We argue that only when the observed change exceeds the baseline change rate, one can confidently conclude that directional change is in play and that the ecosystem is shifting to a new composition, possibly as a consequence of disturbance events or changed environmental conditions (Valencia et al. 2020).

Yet, both quantifying interannual variability and the directional change of plant communities is difficult due to the confounding effects of imperfect sampling. When the same vegetation plot is resampled after one or more years, pseudoturnover might occur as previously missed species are discovered, and previously recorded species are either overlooked or assigned inconsistent cover values. This might happen for several reasons (Bacaro et al. 2009; Morrison 2021), including an imprecise relocation of the surveyed plot (Kopecký and Macek 2015), observer bias (Boch et al. 2022; Morrison et al. 2024), or seasonal bias, that is, the temporal mismatch between the phenological status of certain species groups and the time of the year sampling is taking place (Hédl and Chudomelová 2020; Jandt et al. 2022). Some groups of species, such as spring ephemerals, might be completely missed out in case of an early onset of the growing season after a mild winter, even if the vegetation plot is being resampled exactly on the same dates every year. When one is interested in disentangling the relative importance of interannual variability and directional change, it is crucial to minimize the confounding effects of pseudoturnover.

In practice, all sources of change are likely to act simultaneously, each with a different magnitude depending on the context. A relatively high interannual variability, for instance, has been observed both in treated and untreated samples in a 4-year tree litter removal experiment in the Czech Republic (Vild et al. 2015), as well as in a N-addition experiment in temperate hardwood forests in the Eastern USA (Gilliam et al. 2016). Similarly, inter-annual fluctuations in climatic conditions, especially late winter temperature, have been linked to temporal variation in seedling recruitment in a 16-year litter removal experiment in a mixed oak–pine forests in southern Poland (Dzwonko and Gwronski 2002). Furthermore, quantifying interannual change is complicated by the occurrence of both self-reinforcing mechanisms, when most species respond synchronously to environmental fluctuations, and compensatory dynamics, when the increases or decreases of some species are compensated by changes in the relative abundance of others (Lepš et al. 2019; Valencia et al. 2020). Also, pseudoturnover might be substantial: a recent review reported that interobserver bias might account for up to 30% of species turnover when two observers were sampling the same vegetation plot (Morrison 2016; Morrison et al. 2024). Quantifying each of these components of change is challenging, however, as they can be difficult to disentangle.

The signal of directional change will be stronger when forest ecosystems adjust to the new environmental conditions created by a disturbance event. Disturbance might kickstart succession, that is, a more or less predictable change in forest composition and structure. Succession can be understood as the slow turnover between pioneer light-demanding species, which quickly colonize after disturbance, and shade-tolerant species, which slowly outgrow, outlive, or outcompete pioneer species (Pickett and White 1985). Yet, succession is much less predictable than previously thought (Kulakowski et al. 2017), and criticisms have been moved to purely deterministic models of forest dynamics (Chiarucci et al. 2010). Not only does succession depend on the agent of disturbance (e.g., fire, windstorm, pest, logging), its size, severity, and return interval (Seidl et al. 2017). But stochastic processes and historical contingencies reroute communities on alternate pathways of development depending, for instance, on the species composition before disturbance (Naaf and Kolk 2016), or the spatial distribution of biological legacies (Donato et al. 2012). Many open questions remain, therefore, about the timing and pace of vegetation change after disturbance. How soon after disturbance do forest communities start adjusting to the new conditions? What is the yearly rate of species turnover after disturbance? For how long will this change last? To what extent are the observed changes clouded by pseudoturnover? Answering these questions will help design management schemes better suited at mimicking natural forest dynamics and maximizing the ability of managed forests to provide nature-based solutions (Kermavnar et al. 2021; Seddon 2022).

Given forests' slow pace of compositional change, the best source of data to study their temporal dynamics are vegetation plot time series (Jandt et al. 2022; Sabatini et al. 2023; Knollová et al. 2024). Ideally, this should be both decade-long and yearly-resolved, that is, repeated over several consecutive years. While a number of such vegetation time series exist (Sperandii et al. 2022), most time series are indeed sparse and lack a yearly resolution (Jandt et al. 2022; Knollová et al. 2024). By providing multiple assessments of the composition of the same community over short time intervals, yearly time series have several advantages over sparse time series. First and foremost, they disclose the possibility to study not only long-term trends in vegetation, but also to assess species dynamics and community stability (Lepš et al. 2019; de Bello et al. 2020; Valencia et al. 2020). Second, long and yearly-resolved time series also allow quantifying the baseline change rate of the system, for instance by comparing the year-to-year change rate in disturbed versus undisturbed plots (Valencia et al. 2020). Third, yearly-resolved time series can also be used to control to a certain extent for pseudoturnover, for instance by reducing the chance that a species is missed altogether, or by tracking the occurrence of newly appeared species to make sure that these are genuine additions to the community, and not commission errors by the surveyors. Long and yearly-resolved time series can therefore provide a more accurate understanding of how vegetation communities are changing over time and help control for pseudoturnover by teasing apart genuine ecological dynamics from noise.

Here, we collected and used a yearly time series of permanent vegetation plots resampled for 13 consecutive years to investigate the successional trajectory of the herb-layer vegetation after a small-scale natural disturbance in a Southern-European beech forest after controlling for pseudoturnover. We have three overall research goals:

1. Derive an approach to control for and quantify the magnitude of pseudoturnover leveraging the temporal resolution of the time series.
2. Compare temporal turnover across disturbed and undisturbed sites and quantify the relative importance of interannual variability and directional change (=succession), before and after controlling for pseudoturnover;
3. Assess the timing, pace, and magnitude of vegetation change after disturbance.

We focused on the herb layer, which hosts most of the diversity in our study system (Spicer et al. 2020) and is normally the first layer to respond to disturbances with cascading effects on the entire trophic network and other key ecosystem processes, such as tree and shrub recruitment (Royo and Carson 2006). While the determinants and spatial patterns of the herb layer are relatively well understood, our understanding of its temporal dynamics is lagging (Kermavnar et al. 2021; Kermavnar and Kutnar 2024).

2 | Methods

2.1 | Study Area

On June 14, 2012, we witnessed the collapse of a large European beech (*Fagus sylvatica*) tree having a diameter at breast height (DBH) of 111 cm during a mild windstorm, and the consequent opening of a ca. 400 m^2 canopy gap (Figure 1). The canopy gap is located at 1240 m elevation on the right bank of the Venacquaro stream, a forested mountain valley in the Gran Sasso and Monti della Laga National Park (central Apennines, Italy) (42°30′00″ N 13°30′40″ E). The surrounding forest stand belongs to the habitat 9210*—Apennine beech forests with *Taxus* and *Ilex*, a habitat of priority interest according to the EU Habitats Directive (92/43/EEC). The stand is an old coppice with standards, which transitioned to high forest. The collapsed beech tree was probably one of the standards left after the last coppicing event. The stand is dominated almost monospecifically by European beech with few scattered individuals of *Acer pseudoplatanus* and *Salix caprea* (Sabatini et al. 2018). From the geological point of view, the area is characterized by the outcrop of the Laga Formation, composed of alternating arenaceous and marly-arenaceous layers of Miocene origin. The valley bottom, however, is covered by thick limestone scree deposits collapsed from the neighboring Pizzo di Intermesoli mountain. The annual average temperature registered at the closest meteorological station of Pietracamela (1000 m a.s.l.) is around 10.5°C. Average annual precipitation is higher than 1050 mm (Calamini et al. 2011).

2.2 | Sampling Design and Collected Data

A few days after the opening of the canopy gap, we established nine permanent quadrats, 5 m × 5 m in size, which we resurveyed yearly for 13 consecutive years (2012–2024), always in the period comprised between June 15 and July 15 to ensure both vernal and summer species were detected. Three quadrats were positioned inside the canopy gap, three at the gap margin, and three in the forest interior. The three quadrats within the canopy gap were located five meters from the gap center in three cardinal directions (S, N, W). It was not possible to establish a sampling quadrat five meters east of the gap center due to the physical encumbrance of the foliage of the crashed tree. The margin and forest interior quadrats were located, respectively, at 25 m and 45 m from the gap center, along the same directions, with one exception: the quadrats located 25 and 45 m west of the canopy center were replaced by quadrats located 25 and 45 m east of the center to avoid a forest trail (Figure 2).

We sampled vegetation in three different layers: tree (height > 3 m), shrub ($1.3 < \text{height} \leq 3$ m) and ground layer (height ≤ 1.3 m). After recording the presence of each species, we visually estimated their cover using an ordinal cover class scale with class limits 0.5%, 1%, 2%, 5%, 10%, 15%, 20%, and thereafter every 10% up to 100%. Cover values were assigned separately for each layer in the field but aggregated at the quadrat level for statistical analysis.

In each quadrat, we also recorded a set of micro-topographical variables, namely: slope, aspect, topographical position (ridge top, upper slope, mid slope, lower slope, valley, flat area), and percentage cover of outcropping rocks and stones. For each quadrat, we also took and averaged four readings of a hemispherical densiometer directed in the cardinal directions to estimate the openness of the canopy ("canopy openness" hereafter), as an indirect measure of light available at the forest floor.

FIGURE 1 | Italian Ministry of University and Research Creation (2012) and following colonization of the canopy gap by short (e.g., *Sanicula europaea*, *Galium sylvaticum*) and tall herb (e.g., *Atropa belladonna*) species over the years. In 2022, another neighboring large beech tree collapsed, partially covering one of the quadrats in the canopy gaps with deadwood and leading to the lateral expansion of the canopy gap. Photos: F.M. Sabatini.

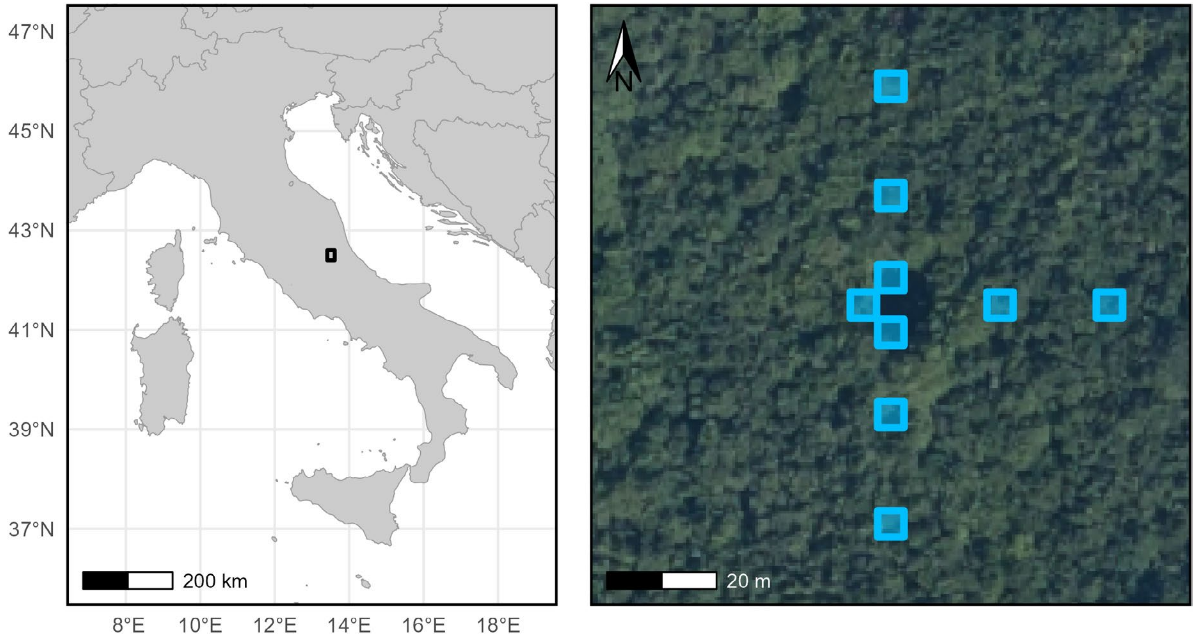

FIGURE 2 | Position of the study site (left) and sampling scheme (right).

2.3 | A Matrix Decomposition Approach to Control for Pseudoturnover

Pseudoturnover might stem from three main potential errors: observer error, relocation error, and seasonal bias (Morrison 2021). While we do not expect observer error to play a major role in our study, since the resurvey was conducted by the same person every year (FMS), relocation error and seasonal bias may. Only the center of the canopy gap was permanently marked in the field, which means that our nine quadrats were relocated through ground measurements that might result in a relocation error estimated to be ~1 m and in the omission or commission of species. Seasonal bias can also play a role. While we resurveyed our quadrats always at the same time of the year, we noticed that the phenological status of spring ephemerals varied from year to year, possibly due to the different timing of the onset of the growing season.

The density of our time series allowed us to account for and quantify the impact of pseudoturnover in a manner that is not available to sparse vegetation time series or vegetation plots resurveyed only once. We did so through a matrix decomposition approach, where the original species × quadrat|year matrix (which we call **T** from "Total") was additively decomposed into two new matrices, one accounting for apparent temporary turnover (matrix **P**) and one for the residual turnover (**R**), where **P** and **R** have exactly the same dimensions as **T**, and $\mathbf{P}+\mathbf{R}=\mathbf{T}$. Every quadrat × year combination was considered as an individual row in each of these three matrices.

To calculate **R**, we used a 3-year moving window to pool species observations across consecutive years. In case a species was recorded in a given quadrat both at t–1 and at $t+1$, but not at year t, we assume that the species was overlooked (omission error) at year t and assigned it a cover equal to the maximum cover in the 3-year moving window in **R**. Similarly, if a species was observed at year t, but neither at year t–1 nor $t+1$, we assumed this was a commission error and considered that species absent in **R**. To avoid shortening the time series, **R** maintained the observed values from **T** for both the first and last year of the time series. The matrix **P**, calculated as **T**–**R**, therefore returns a matrix of turnover that we considered as being purely apparent and interpreted as the signature of pseudoturnover. We could then quantify the relative contribution of apparent turnover (**P**) to the total variation of the observed species composition (**T**) by decomposing the total variance of **T** as:

$$S_{\mathrm{T}}^2 = S_{\mathrm{R}}^2 + S_{\mathrm{P}}^2 + 2 \times S_{\mathrm{RP}}$$

where S_{RP} is the covariance between **R** and **P**. The variance of each of these matrices, was calculated as the sum of the squared deviations from the column (=species) means, divided by the number of sites minus 1 (Legendre and De Cáceres 2013). We considered both the variance of **P** and the 2× covariance between **R** and **P** as variance components that collectively account for the magnitude of pseudoturnover. Because calculating variance components on raw species abundances corresponds to using the Euclidean distance when calculating the dissimilarity between sites, which is not appropriate for compositional data, we applied the Hellinger transformation to matrix **T**, before decomposing it additively into **R** and **P** and performing variance decomposition (Legendre and Gallagher 2001).

The specific moving-window approach we adopted for calculating **R** is just one possibility among many and may not be appropriate for all situations. For instance, an annual species may legitimately occur only at year t but be absent at year t–1 and $t+1$. While we note that annual species are quite rare in our study system, we also concede that our approach would incorrectly consider this a commission error and correct for it. Similarly, if one is interested in the part of pseudoturnover depending on seasonal bias, a specific correction approach could be defined for those species most likely to be overlooked, that is, spring ephemerals.

For this reason, we also calculated the relative contribution of pseudoturnover to overall species composition variability when (1) excluding therophytes from the moving window correction, and (2) when applying the moving window correction exclusively to spring ephemerals. These comparisons are given only as an example, and while the numerical results of the analysis are reported in the appendices for comparison, in the rest of the main text we will focus mostly on the results based on the main correction approach.

Our 3-year moving-window approach shares similarities with a previous variance decomposition approach based on the calculation of three-term local variance in a moving-window framework (Lepš et al. 2019; Valencia et al. 2020). The similarity derives from the same intuition that long and yearly-resolved time series can help to disentangle different drivers of change of species composition. But while our approach was meant at controlling for the effect of pseudoturnover when quantifying the relative importance of directional change and interannual variability, the three-term local variance approach was developed for a different purpose, that is, for detecting patterns of synchronicity\asynchronicity among species after controlling for directional change (Lepš et al. 2019; Valencia et al. 2020).

2.4 | Quantify the Relative Importance of Interannual Variability vs. Directional Change After Controlling for Pseudoturnover

To quantify the relative importance of interannual variability versus directional change across disturbed and undisturbed quadrats, we decomposed the total variation of **R** using a Permutational Analysis of Variance (PERMANOVA) with the function "adonis2" from the *vegan* package in the statistical software R v 4.2.2 (R Development Core Team 2022). We applied the formula

$$\mathbf{R} \sim \text{Treatment} \times \text{Year} + \text{Quadrat}$$

In this way, we decomposed the variation of **R** into five terms: (1) treatment (i.e., gap, margin, forest interior), (2) year, (3) the interaction between treatment and year, (4) quadrat, and

(5) residual. Any directional change triggered by disturbance should increase the variation explained by Components (1) and (3). Component (1) accounts for the cumulated differences between quadrats across treatments, while Component (3) accounts for the different directional changes of the species composition over time in the quadrats across treatments. Both Components (2) and (5) account for interannual variability. The “year” Component (2) explains all those changes that are coordinated across all quadrats, for instance those related to yearly variation in the weather conditions across all quadrats. Given the model formulation, the Component (5) quantifies the quadrat-specific differences across years, which relate to metacommunity dynamics across quadrats, for instance, immigration, recruitment, or extinction in a given quadrat. Finally, Component (4) (quadrat) was considered as a random effect and used as a stratum in the randomization algorithm. It represents the quadrat-to-quadrat variation that does not depend on treatment. Here we note that summing the variance of these five components to the variance of **P** and twice the covariance between **R** and **P** equates to the total variance of **T**.

To better understand the confusing effect of pseudoturnover, we compared the results of decomposing the variation of the matrix **R** (i.e., after controlling for apparent turnover), versus the results of decomposing the variation of the matrix **T** (i.e., without controlling for apparent turnover). We expect that controlling for apparent turnover should reduce the estimated interannual variability, both the part which is consistent across all quadrats (component “year”), and the part which is unique to each quadrat (component “residual”).

2.5 | Assess the Timing, Pace, and Magnitude of Vegetation Change After Disturbance

To assess the timing and pace of vegetation change after disturbance, we built two helical graphs based on the compositional matrix **R**: one for species richness and one for the total cover of the herb layer. Helical graphs show the state (on the y axis) of a variable and its rate of change between measurements (on the x axis), years in our case (Thouverai et al. 2023). Being the x-axis a representation of annual change, a curve moving to the right indicates that the rate of change of the variable of interest is increasing between two points in time, while a curve going to the left indicates that the rate of change is decreasing. To improve the visualization of the data, we based our helical graphs on the moving average calculated for the 3 years preceding each point plotted. Moving averages were further smoothed using the “loess” (locally estimated scatterplot smoothing) function in R, with a span parameter of 0.75.

To visualize change in species composition, we used the *metaMDS* function from the R package *vegan* (Oksanen et al. 2022) to compute a non-metric multidimensional scaling (NMS) based on the Bray–Curtis distance. Using two axes ($k=2$) proved sufficient to return a level of stress, which we deemed acceptable for our visualization purposes (stress = 0.14). To characterize the two axes in terms of the dominant species, we passively fitted the matrix of species composition on the NMS ordination using the *envfit* function, also from the *vegan* package.

To compare the temporal turnover across disturbed and undisturbed quadrats, we used mixed effect models. As response variables, we used the difference in (1) species richness (DeltaSR) and (2) total cover (DeltaCov) of the herb layer between a given year t and the year of disturbance t_0 (=2012). As predictors, we used treatment (three levels: gap, margin, forest interior), time since disturbance as t–t_0 (DeltaYear) and the interaction between the two. DeltaYear was converted to natural logarithm as log(DeltaYear + 1) to improve model fit. To account for the nested structure of the data, we used quadrat identities as a random effect. To account for temporal autocorrelation, that is, the fact that the similarity between the repeated surveys of each quadrat decreases with the time interval (lag) between the measurements, we incorporated a first-order autoregressive structure into the model, using the “CorAR1” correlation structure from the nlme package (Pinheiro et al. 2018). Our final models were then:

$$\mathrm{lme}(Y \sim \mathrm{Treatment} \times \mathrm{Log(DeltaYear)}, \mathrm{random}$$
$$= (\sim 1|\mathrm{Quadrat}), \mathrm{correlation} = \mathrm{corAR1}(\mathrm{form} = \sim 1 \ \ |\mathrm{Quadrat}))$$

where Y was either DeltaSR or DeltaCov. We ran this model both for pseudoturnover-corrected compositional matrix **R** and on the uncorrected matrix **T** for comparison.

3 | Results

During the 13 years of monitoring, we found a total of 86 vascular plant species, 31 of which were exclusively found in the canopy gap, three were exclusive of the gap margin, and eight of the forest interior. In total, we found 70 species in the quadrats located under the canopy gap, 39 in those at the gap margin, and 48 in the forest interior. The species we found the most often were: *Cardamine bulbifera*, *Sanicula europaea*, *Viola reichenbachiana*, *Galium odoratum*, and *Geranium robertianum*. The species occurring with the highest average cover were *Atropa belladonna*, *Galium odoratum*, and *Sanicula europaea*. Over the 13-year period, canopy openness remained consistently and continuously low for the quadrats in the forest interior (range 1.5%–13.8%) and at the gap margin (range 0.5%–13.2%), compared to the much higher values observed in the canopy gap (range 14.5%–44%) (Appendix S1).

3.1 | Relative Importance of Interannual Variability and Contribution of Pseudoturnover

After correcting our species × quadrat|year matrix of species composition with a 3-year moving window, we found that apparent turnover, as a proxy for pseudoturnover, accounted for 0.4% of total variation. In absolute numbers, the total variance of T (Var(T)) was 61.8, and was decomposed as the sum of the three components Var(R) = 61.5, Var(P) = 117.9, and $2 \times \mathrm{Cov}(RP) = -117.5$.

Overall interannual variability and directional change accounted for almost the same amount of variation. Taken together, the two components of interannual variability explained 26.7% of variation, 20.8% stemming from quadrat-level interannual variability (component residual) and 5.9% from interannual

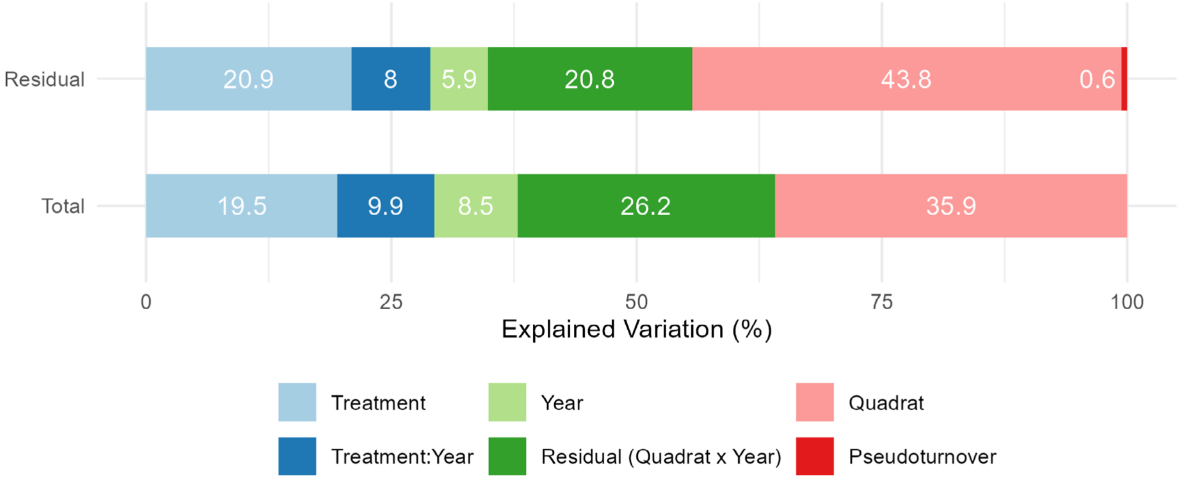

FIGURE 3 | Variation decomposition of the species composition of the herb layer through PERMANOVA before (bottom) and after (top) accounting for pseudoturnover. Numbers in percentage. Components "Treatment" and "Treatment: year" quantify the contribution of directional change triggered by disturbance. Components "Year" and "Residual" account for interannual variability. The component "Quadrat" was used as a stratum in the randomization algorithm and represents the quadrat-to-quadrat variation that does not depend on treatment.

variability coordinated across quadrats (component year). The two components of directional change accounted for 28.9% of total variation, 20.9% deriving from the treatment component, that is, the cumulated differences between gap, margin, and interior quadrats, and 8.0% from the interaction between treatment and year. The term quadrat, representing the initial plot-to-plot variation, accounted for the remaining 43.8% variation (Figure 3, top).

Comparing these results to those obtained from decomposing the matrix *T*, we found that not controlling for pseudoturnover would result in an overestimation of interannual variability, which would increase to 34.7% (from 26.7%): the residual and the year components increased to 26.2% and 8.5%, respectively. The importance of directional change would also be overestimated, but only slightly, with the increase of the treatment-year component (to 9.9%) being partially compensated by a decrease of the treatment component (to 19.5%). Not controlling for pseudoturnover would also result in an underestimation of the quadrat component (Figure 3, bottom).

The two alternative correction approaches accounting for annual species and spring ephemerals, respectively, returned very similar results to our main correction strategy, although with a slightly higher variation associated with pseudoturnover, namely 1.3% when excluding therophytes from the correction, and 3.6% when correcting for spring ephemerals only (Appendix S2, Appendix S3).

3.2 | Timing, Pace and Magnitude of Vegetation Change After Disturbance

In the years immediately after disturbance, the herb layer reacted vigorously to the changed light conditions. In the quadrats located in the canopy gap, we observed a sustained increase in species richness over the 13-year study period, which grew from 11.0 species per quadrat on average in 2012 to 23.3 in 2019, before slightly decreasing to 20 in 2024. Species richness remained constant in the other two treatments: from 9.0 to 8.3 species on average at the gap margin, and from 12.0 to 11.0 species on average in the forest interior. The yearly rates of change were particularly high in the first 7 years after disturbance in the canopy gap, with the maximum increase observed in an individual quadrat being as high as +6 species/year. The increase in species richness slowed down after 2019 and reached a plateau afterward (Figure 4a). Even if the quadrats at the gap margin and in the forest interior did not show substantial net changes in species richness over the 13-year study period, there were relatively strong yearly fluctuations in species richness, with quadrat-level yearly change rates comprised between −4 and +3 species per year (Figure 4c).

Changes in the total cover of the herb layer were even more considerable. Total cover increased from 9.3% to 85% on average in the canopy gap quadrats, while it decreased slightly in the other two treatments: from 11% to 6.3% at the gap margin, and from 11.5% to 7.7% in the forest interior. The increase in total cover was particularly sustained until 2018, with quadrat-level yearly rates of change consistently higher than +20% (Figure 4b). After 2018, quadrat-level total cover dropped from 97% to 68% on average across the three quadrats in the canopy gap, before increasing again in 2023, possibly after the collapse of the tree neighboring the initial canopy gap. The other two treatments showed very limited yearly fluctuations in total herb-layer cover across the whole study period (Figure 4d). Temporal trends were similar when using compositional data not corrected for pseudoturnover, although in the case of species richness, uncorrected data returned a much higher year-to-year variation (Appendix S4).

The NMS returned a similar picture (Figure 5). The vegetation in the gap diverged strongly and quickly from the initial conditions and moved toward the left end of the NMS axis 1, which was significantly ($p < 0.001$) associated with an increased occurrence of *Fragaria vesca, Viola reichenbachiana, Galium odoratum, Sanicula europaea, Atropa belladonna, Rubus idaeus, Primula vulgaris*, and *Lactuca muralis* (not

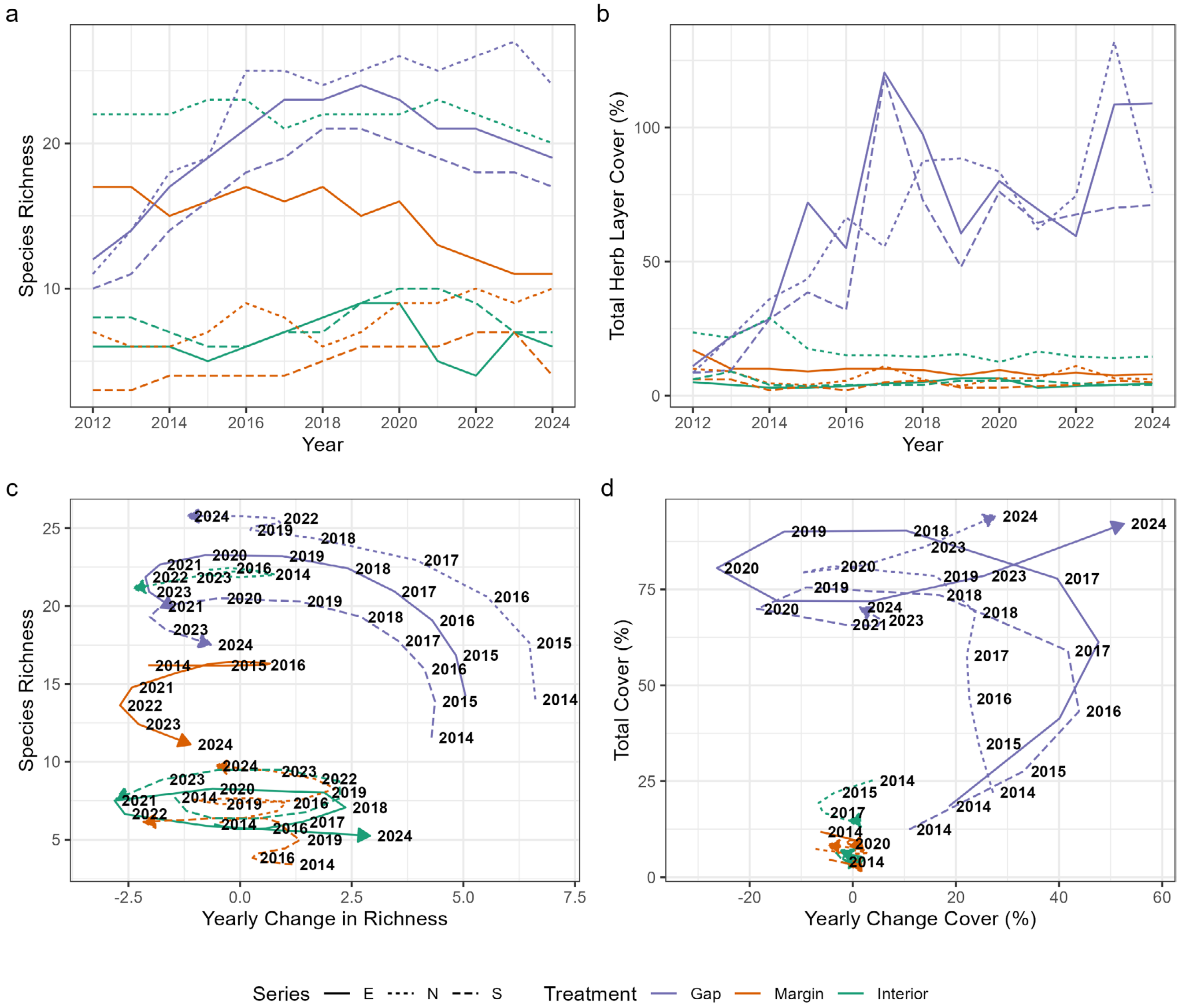

FIGURE 4 | Change in species richness (a) and total cover (b) with time, and helical graphs of species richness (c) and total cover (d). The graph shows the trajectory of each individual plot, as identified by the combination of treatment (Gap, Margin, Interior), and cardinal position compared to the canopy gap center (East, North, South).

shown). The herb layer at the gap margin and in the forest interior, while varying substantially from year to year, did not show any clear directional change on either of the two NMS axes, and consistently remained on the right end of the NMS axis 1. Trends were qualitatively similar when using uncorrected data (Appendix S5).

3.3 | Temporal Turnover Across Disturbed and Undisturbed Quadrats

When regressing DeltaSR, that is, the difference in species richness between year t and t_0 (=2012), against time we found no significant difference between treatments but a strong significant effect of the interaction between treatment and year (Figure 6a). In canopy gaps, DeltaSR increased by 4.3 units for each unit increase in log(year + 1), which translates to an increase of 3.0 species between year 2012 and 2013, 0.8 species between year 2016 and 2017, and 0.3 species between year 2023 and 2024. Yearly increases were negligible in the other two treatments. The autoregressive coefficient was 0.87, indicating a strong correlation between residuals at year t and $t+1$.

Results were qualitatively similar when regressing DeltaCover against time (Figure 6b). Also in this case, we found no significant effect of treatment, while the interaction between treatment and year was strong and significant. For each unit increase in log(year + 1), the increase in total cover was equal to +33.2%. This translates to a 23.0% increase between year 2012 and 2013, a 6.1% increase between year 2017 and 2016, and a 2.5% increase between year 2023 and 2024. The autoregressive coefficient was much weaker in this case, being 0.04. Results were qualitatively similar when using uncorrected data (Appendix S6).

4 | Discussion

Vegetation changes at multiple temporal scales, seasonal, yearly, and decadal, as the cumulated effect of weather patterns, variability in climatic conditions, metacommunity dynamics, and directional change related to succession or modified environmental conditions (Kermavnar and Kutnar 2024; Bakker et al. 1996; Pickett et al. 2013). Decomposing these sources of variation is necessary to understand whether the change in species composition observed between two resurveys exceeds the baseline change rate, that is, the year-to-year fluctuations in species composition and cover that are to be expected under relatively stable environmental conditions. Yet, any attempt to compare directional change and interannual variability needs to account for pseudoturnover, as it can cloud this comparison and introduce bias. Here, we derived an approach based on matrix algebra to disentangle the effect of different sources of vegetation change, including pseudoturnover, which can be applied to long and yearly-resolved time series of resurveyed vegetation plots. We applied this approach to quantify the timing, pace, and magnitude of the compositional change of the herb layer in a European beech forest for the first 13 years after a fine-scale disturbance event. We found that pseudoturnover accounted for a small but not negligible part of the observed vegetation change and demonstrated that it can bias estimates of the interannual variability. Even if we observed a quick and sustained change in herb-layer composition following disturbance, disturbance-induced directional change produced as much compositional variation as interannual variability over the study period.

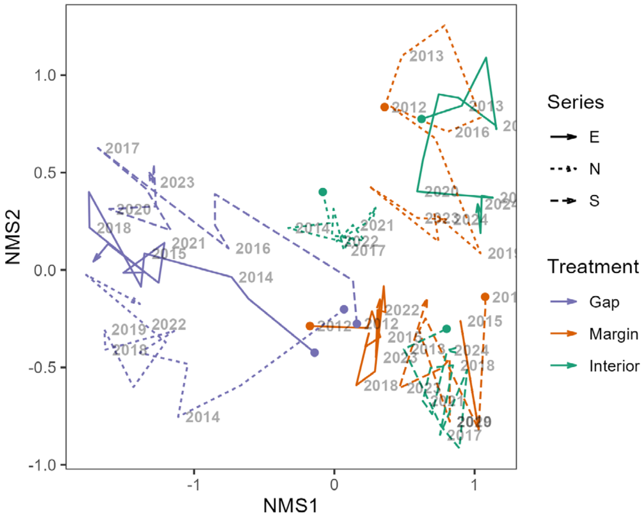

FIGURE 5 | Temporal trajectory of each sample plot in a Non-metric Multidimensional Scaling (NMS) ordination based on plot-to-plot Bray–Curtis dissimilarity and compositional data. The graph shows the trajectory of each individual plot, as identified by the combination of treatment (Gap, Margin, Interior), and cardinal position compared to the canopy gap center (East, North, South).

While pseudoturnover accounted for a small amount of variation overall, our results suggest that it may disproportionately increase the perceived magnitude of interannual variability. If interannual variability is to be taken as the benchmark for assessing the magnitude of directional change on vegetation, the finding that neglecting pseudoturnover might result in overestimating baseline change rates is noteworthy. It implies that pseudoturnover could confound our ability to perceive directional change through monitoring, undermining our ability to take timely action. While the variation associated with pseudoturnover in our work was small compared to the 10%–30% variation reported by Morrison (2016), here we note that our resurvey was conducted always by the same observer and

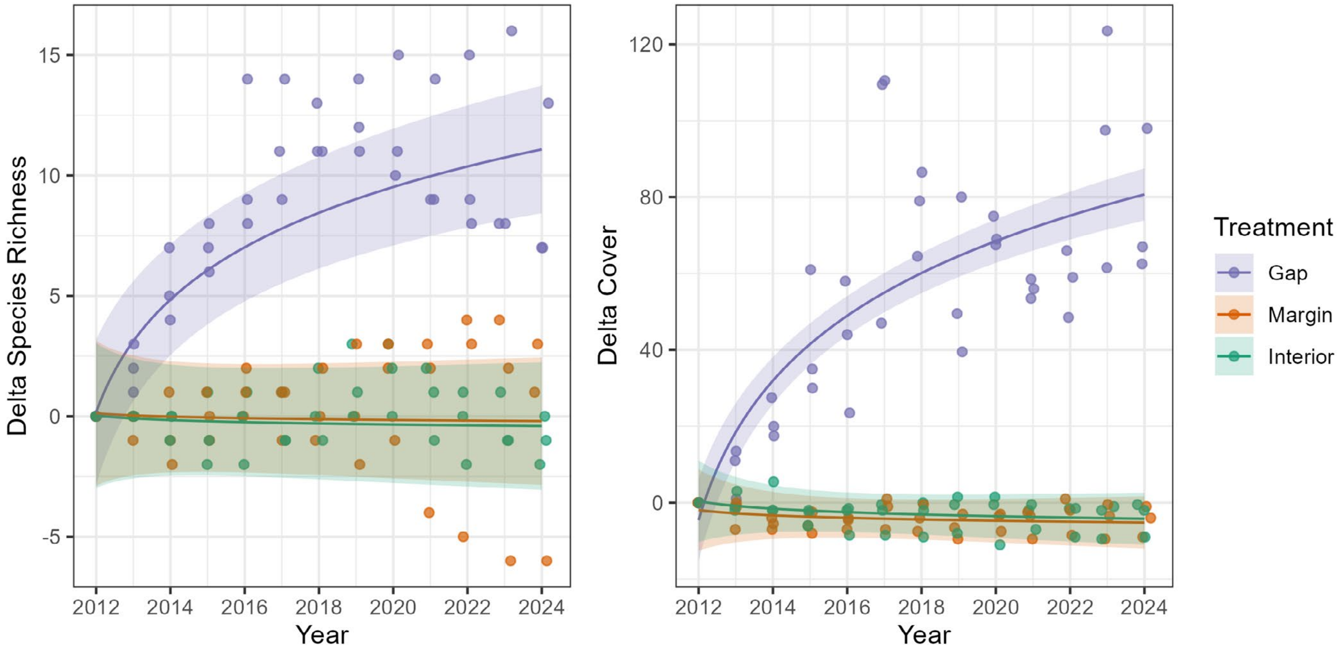

FIGURE 6 | Relationship between delta species richness (left) and delta cover (right) and log-transformed delta year, as modeled through mixed effect models with first-order autoregressive structure. Delta species richness (cover) was modeled as species richness at year t minus species richness at t_0 (i.e., 2012).

that quadrats could be relocated in the field with a precision (~1 m) that is higher than in most resurvey studies where plots are not marked permanently. In resurvey studies characterized by higher interobserver error (e.g., Lepš and Hadincová 1992; Bacaro et al. 2009) or higher location uncertainty, accounting for pseudoturnover becomes even more compelling.

Incidentally, we note that our approach does not exclude the possibility that pseudoturnover, rather than increasing the total variance of a study system, decreases it and leads to an underestimation of the baseline change rate and a consequent overestimation of the magnitude of directional change. Mathematically, this can happen when the sum between the variance of the pseudoturnover correction matrix **P** and twice the covariation between **P** and the matrix of corrected species composition **R** ($\mathrm{Var}(\mathbf{P}) + 2 \times \mathrm{Cov}(\mathbf{RP})$) returns a negative value. An example could be a study system where omission errors dominate and small annual species are systematically overlooked during resurveys, so that the baseline change rate from year to year is underestimated. This implies that the decomposition approach that we propose here could also provide insights into the dominant source of the pseudoturnover in the data, but only as long as the correction approach is properly designed for the system being studied.

The share of compositional variation attributed to interannual variability was comparable to that attributed to directional change in our study system. This was an unexpected finding, given that the herb layer of European beech forests is mainly composed of long-lived species, and its year-to-year dynamics has often been neglected in forest vegetation change studies, at least compared to the attention devoted to studying directional change, especially after disturbance (Kermavnar and Kutnar 2024). In our study system most of the year-to-year variation in species composition was at quadrat level (Quadrat × Year component), rather than coordinated across all quadrats (Year component). Besides, we found a higher temporal autocorrelation for species richness, compared to total quadrat cover. This suggests that, rather than being driven by year-to-year variability in drivers affecting all quadrats alike, such as weather patterns or increasing temperatures, most of the interannual variability in our system depends on stochastic, quadrat-level metacommunity processes of dispersal, colonization, and extinction, possibly affecting species abundances more strongly than species occurrences. It also suggests that the herb layer is more dynamic than previously thought, not just in the canopy gap, where succession triggers directional change, but also in the forest interior where environmental conditions are relatively stable. A similarly high year-to-year dynamics within plots was observed across a range of study systems, and linked to either weather fluctuations or population dynamics (Dzwonko and Gwronski 2002; Vild et al. 2015; Gilliam et al. 2016; Fischer et al. 2020). Whatever the underlying driver, it is likely that high baseline change rates may contribute to the long-term stability of the system. This is predicted, for instance, by the “carousel model,” where high temporal mobility of species in relatively homogeneous habitat conditions was hypothesized to be a key mechanism for maintaining biodiversity (van der Maarel and Sykes 1993). The asynchronous response of species to environmental fluctuations has also been linked to compensatory dynamics which stabilize ecosystem biomass (Valencia et al. 2020).

The herb layer of our beech forest reacted vigorously to the opening of a small canopy gap, but directional change was limited to the gap itself, without reverberating to the gap margin and to the forest interior. Change was particularly sustained in the first 7 years after disturbance before slowing down and triggered both an increase in species richness and a turnover in species composition. The canopy gap was quickly colonized by species adapted to more open conditions, such as *Atropa belladonna* and *Rubus idaeus*, but experienced also a stark increase in cover by shade-tolerant species also found in the forest interior, such as *Sanicula europaea* and *Galium odoratum*. The fact that vegetation in quadrats at the gap margin behaved as in the forest interior was unexpected. We expected that the increased light availability due to the gap opening would affect also the herb layer in the gap margin, according to the gap-partitioning hypothesis that states that species with different requirements establish in different parts of the same gap, including the edge (Perry et al. 2008). Considering that light availability depends on the ratio between canopy height and gap radius (Hagemann et al. 2022), this was probably due to the small gap size. Gap size was found to be one of the main determinants of herb-layer response to canopy openings, being most vigorous in large gaps across a range of forest systems (Promis et al. 2012; Ravnjak et al. 2022). However, we note that our study area is at the bottom of a river valley flowing northward from a high mountain peak (Pizzo di Intermesoli, 2635 m a.s.l.), whose shade might further explain the limited impact of gap creation on the light availability at the gap margin. For these reasons, probably the increase in light availability at the gap margin was insufficient to trigger any meaningful directional changes in the herb layer. In general, 13 years after disturbance, the system has not yet returned to pre-disturbance conditions, nor does it seem to have reached a new steady state. Indeed, canopy openness is still high, and no new trees have recruited to the canopy layer.

While the repeated resampling of permanent quadrats over 13 consecutive years makes our dataset very useful to tackle some crucial questions concerning the resilience and temporal response of the forest herb layer to disturbance, our study has some clear limitations. The first one is due to the limited spatial replication, being the whole study based on nine quadrats and one canopy gap only. Clearly, this poses a severe limit to the possibility of generalizing our results to other canopy gaps in the same forests, not to mention other forest types. But a small sample size is a trade-off for maintaining permanent plots in the long term, which is no easy task. Discipline (Bakker et al. 1996) and long-term institutional support and funding (de Bello et al. 2020) are required to maintain a vegetation-plot time series in the long term, which becomes increasingly difficult when sampling effort increases. In addition, if forest monitoring is intended to provide reliable trends over a broad scale beyond the local monitoring sites, design-based issues should be properly taken into account (Ferretti and Chiarucci 2003). Furthermore, we concede that the interpretation of the drivers of the change we observed is to a certain extent speculative, since we could not relate it to any direct measures of environmental change sampled in the field besides light. The last drawback is that our study site, while not directly impacted by human activities, is surely grazed by wild ungulates, which are abundant in the National Park. To what extent herbivores contributed to increasing the year-to-year variability and/or slowed down succession remains a matter of speculation, but they are likely to have a key influence on the system, at least based on evidence from the herb layer of the beech-fir forests of another National Park in the Apennines (Gonnelli et al. 2014).

Notwithstanding these limitations, our study has some clear implications for studying vegetation change. First, it shows that a simple before-after study of vegetation might not return a complete picture of the disturbance-induced changes in the herb layer, given the risk of misinterpreting vegetation dynamics. Rather, the year-to-year dynamics can be substantial and can provide context for interpreting whether the amount of vegetation change observed in a given time interval is stronger than the "normal" interannual variability, and on the degree the observed change has led the system to a new steady-state. Second, we proposed a matrix-based approach that leverages the wealth of data made available by long and yearly-resolved vegetation time series data to control for pseudoturnover and disentangle the effect of different components of change. Controlling for pseudoturnover will ultimately return a clearer picture of vegetation dynamics, limiting the possibility to over- or underestimate the magnitude of any observed directional change. Finally, we showed that interannual variability is quite strong in our system, therefore providing a benchmark to assess the magnitude of any directional change in species composition, be it imputed to succession after disturbance, climate change or any other energy or biogeochemical imbalance.

Author Contributions

F.M.S. conceived the research idea; F.M.S. and M.D.M. collected data; F.M.S. performed statistical analyses; F.M.S., with contributions from M.D.M. and A.C., wrote the paper; all authors discussed the results and commented on the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data needed to reproduce this work can be accessed at https://zenodo.org/records/15196194. The code to reproduce the analysis is stored at https://github.com/fmsabatini/GapNovello.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1.** Comparison of canopy openness evolution over time across treatments. **Appendix S2.** Comparison of the variation decomposition based on PERMANOVA between species composition matrices. **Appendix S3.** Variation decomposition of the species composition before and after accounting for pseudoturnover using three alternative approaches. **Appendix S4.** Change in species richness and total cover with time before correcting for pseudoturnover. **Appendix S5.** Non-metric Multidimensional Scaling (NMS) of compositional data before correcting for pseudoturnover. **Appendix S6.** Relationship between (1) delta species richness and (2) delta cover and time before correcting for pseudoturnover.