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Different ways to success: Plant community trajectories over time and a soil moisture gradient in restored wetlands

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Abstract

1. Ecological restoration is one of the most promising strategies to combat historical wetland losses caused by land use changes. Restored areas are ideal sites to study plant succession and changes in ecosystem functions over time. However, little is known about the influence of restoration on plant succession along environmental stress gradients. Knowing the processes and mechanisms driving the succession over time in contrasting abiotic conditions might provide new insight into the ultimate success of an ecological restoration.

2. Relying on long-term vegetation monitoring, we studied the community succession of 4 plant communities along a restored waterlogging gradient in North-East Italy (from high to low soil saturation level): (i) *Cladium* fens, (ii) low alkaline fens, (iii) *Molina* wet meadows and (iv) dry meadows. We monitored 23 permanent plots distributed along the gradient, spanning from 1 to 21 years since restoration, and 4 plots as target vegetation (natural habitats). We analysed the changes in plant communities in terms of functional traits, diversity and species composition.

3. We found that exotic and annual species decreased in mature stages of restoration while leaf dry matter content increased over time. Nutrient indicator value and leaf area showed opposite trends at the extreme points of the gradient. Across the successional stages, species richness decreased in *Cladium* fens and increased in alkaline fens and meadows. Species composition moved toward target vegetation showing contrasting dynamics between different restored habitats.

4. *Synthesis and applications*. During succession waterlogging stress acts as main abiotic filter, triggering contrasting trajectories of plant communities. This filter seems to be stronger at the extreme points of the gradient generating opposite but faster dynamics than at intermediate conditions. Time and waterlogging promoted a continuous selection of species consistent to target vegetation in terms of richness, functional traits and composition. The evidenced trajectories suggest the need to develop habitat-specific protocols concerning the selection

of restoration site and subsequent management decisions, with particular regard to plant communities at intermediate ecological conditions.

1 | INTRODUCTION

Land use changes are the primary cause of natural ecosystems loss (Ellis et al., 2010; Foley et al., 2011). Among world ecosystems, wetland areas were dramatically reduced in the last centuries, with an estimated global area contraction of about 70% since 1900. Losses have been larger for the inland than the coastal wetlands, mainly due to agricultural drainage (Davidson, 2014), triggering negative feedbacks on both regional and global biodiversity (Leibowitz, 2003). Therefore, the retention of minimum wetland densities is fundamental to maintain present biodiversity levels (Gibbs, 2000) and ecological restoration is increasingly used to address historical wetland losses (Ballantine & Schneider, 2009).

Understanding plant ecological succession is pivotal to provide a means of assessing restoration progress when compared with natural reference sites (Ballantine & Schneider, 2009; Prach & Walker, 2011). For this reason, many studies have focused on changes in plant communities over time in restored sites (e.g. Boscutti et al., 2016; Matthews & Spyreas, 2010), but little is known about changes in trajectories along an environmental stress gradient. Abiotic gradients are pivotal in determining community composition, strongly interplaying with biotic factors (Campbell & Keddy, 2022; Lami et al., 2021; Seabloom & van der Valk, 2003). At early stages of plant community succession, propagule availability and environmental conditions limit plant colonization (Lami et al., 2021; Méndez-Toribio et al., 2020), whereas competition is manly acting in the later stages (Huston & Smith, 1987; Tatsumi et al., 2019). The study of beta-diversity has been demonstrated to be a valuable tool to depict shifts in species composition (Baeten et al., 2012), and also along ecological successions (Puyravaud et al., 2003). Further, functional traits might be key indicators of shifts in plant community assembly (Catano et al., 2021; Meiners et al., 2015), mainly reflecting causal plant–plant, and plant–environment relationships (e.g. Pellegrini et al., 2018). Traits of individual species do not sufficiently reflect community strategies and functions, hence, the assembly rules in communities are typically inferred relying on community functional traits (Kraft et al., 2008). Among abiotic factors, soil waterlogging is considered the main ecological driver in wetlands plant communities, determining both vegetation zonation (Barnett et al., 2015) and functional responses of key species (Pellegrini et al., 2018). The vegetation zonation due to waterlogging at the final ecosystem equilibrium state has been vastly explored, while its effects along an ecological succession have received little attention. Persistent waterlogging is expected to exert higher abiotic filtering favouring native specialist species instead of generalist

exotic and annual species. In this light, studying the response of functional traits and groups (D'Astous et al., 2013), and biodiversity indices (Seabloom & van der Valk, 2003) across successional stages subjected to contrasting levels of waterlogging might elucidate the ecological processes driving changes in plant communities.

Within a theoretical framework, changes in biodiversity across time (i.e. species diversity and composition) result from the interplay between abiotic stress (here expressed by waterlogging) and biotic interactions (here expressed by community traits). Abiotic stress acts as a filter shaping plant communities by favouring some plant traits that, in turn, contribute to shape the communities' biotic interactions and biodiversity. However, the needed time for these dynamics to occur vary along the waterlogging gradient when compared to references sites. These dynamics might have important consequences to evaluate the success of restoration, merging fundamental ecology and applications knowledge.

We analysed the successional trajectories in four main habitat types along a waterlogging gradient in inland restored wetland. We hypothesized that, over time, waterlogging stress triggers different trajectories of plant communities and to be more effective at the extreme points of the gradient. We do also expect that changes in species composition and diversity of restored sites toward target vegetation (natural habitats) have different time-spans according to waterlogging intensity.

Across the successional stages (time since the end of restoration actions), we expected to find: (i) an increase of plant diversity at intermediate waterlogging conditions, (ii) a decrease of exotic and annual species, and this to be accelerated by higher exposure to waterlogging, (iii) changes in community leaf trait syndrome toward mature stages, (iv) community assembly to be driven by species turnover rather than nestedness, in particular in dry conditions.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in the Friuli floodplain across the wetland belt occurring at the transition between the permeable gravel soil of the high plain and the impermeable sandy-pelitic deposits of the low plain, locally known as 'Risorgive friulane' (Figure 1a). The soil transition generates a resurgence of the groundwater that creates a complex system of springs and wetland habitats. The groundwater is cool, with a constant temperature of 10–14°C, alkaline (pH about 7), poor in nutrients but rich in Ca^{2+} and Mg^{2+}. These wetlands are important

FIGURE 1 (a) Study area and (b) location of restored sites in the special areas of conservation investigated. (c) Example of restored wetland site with ideal sampling plots along the waterlogging gradient, represented by (d) four target plant communities.
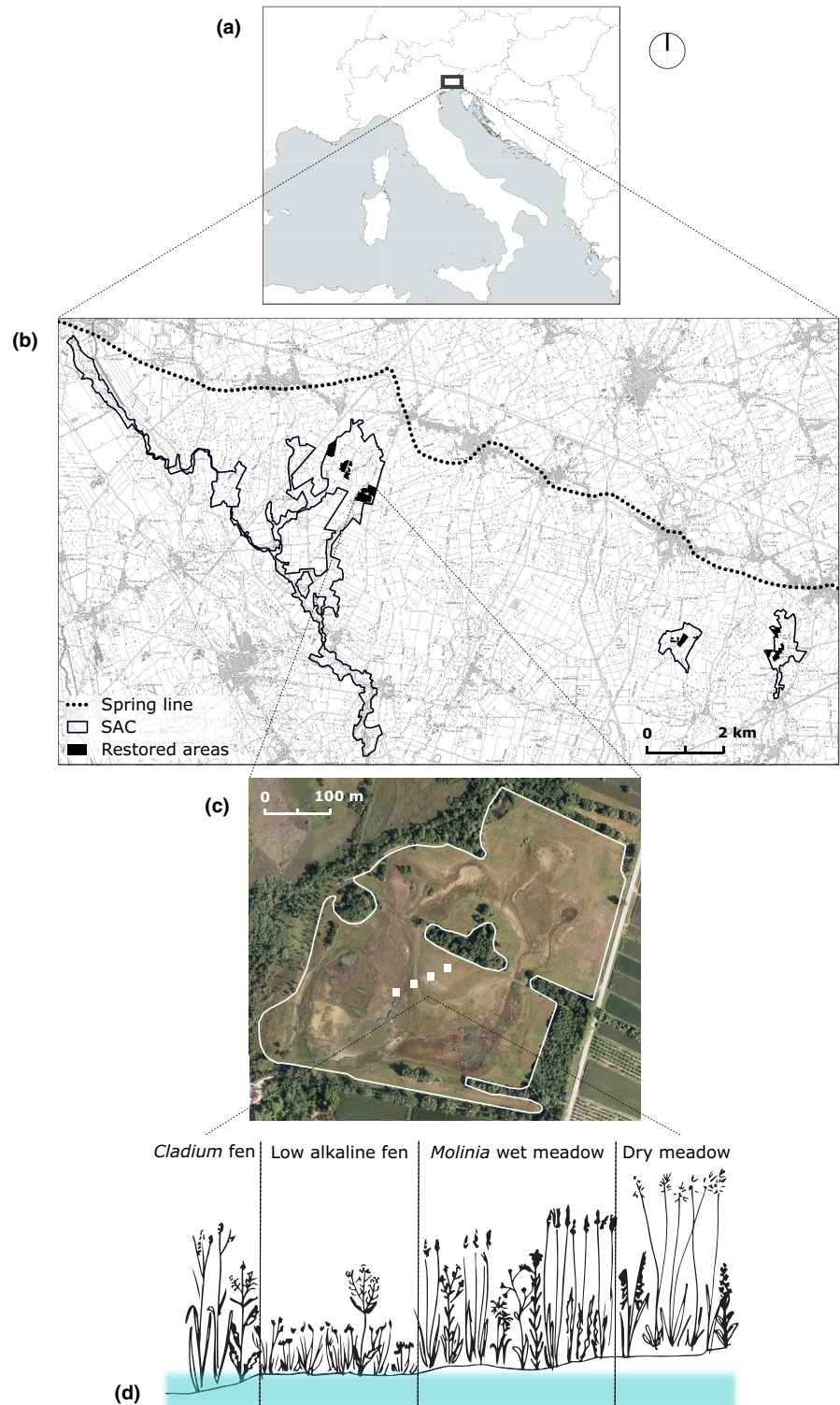
biodiversity hotspots, harbouring several plant and animal species of conservation interest. The study area includes three Special Areas of Conservation (SAC Natura 2000 network, Figure 1b).

The climate is temperate with an average annual temperature of 13.5°C and an average annual precipitation of 1211 mm.

Agricultural drainages occurred between 1930 and 1950 and led to drastic contraction of Friuli springs' wetlands from 6000 to about 200 ha. Most of these drained areas are now agricultural lands.

2.2 | Restoration history

The first restoration started in 1999 with a Life programme which covered only the western site. Subsequently, from 2006 to 2012, within a second Life programme, the restored areas were enlarged and extended to the other sites (overall restored area of about 34 ha). In all the sites, the restoration was conducted in three stages: (1) excavation and removal of agricultural topsoil; (2) landform shaping, consisting

of mechanical shaping aimed at creating the original flood conditions, and (3) seeding with local spontaneous seed mixtures collected from Friuli's natural meadows. Since the restoration actions, all the sites were regularly mowed twice per year with biomass removal.

2.3 | Sampling design and data collection

We used four habitats as restoration target representing the same waterlogging gradient occurring in all the studied wetlands. The corresponding habitat types are included in the annex I of the Habitats Directive 92/43/EEC. Moving from open water to dry land, we selected: *Cladium* fen (7210*—'Calcareous fens with *Cladium mariscus* and species of the *Caricion davallianae*'), low alkaline fen (7230—'Alkaline fens'), *Molinia* wet meadow (6410—'*Molinia* meadows on calcareous, peaty or clayey-silt laden soils'), and dry meadow (62A0—'Eastern submediterranean dry grasslands (*Scorzoneretalia villosae*)') (Figure 1c,d; for details see Appendix S1).

Twenty-three sampling points were randomly distributed in the four restored habitats (i.e. *Cladium* fen, $N = 5$; low alkaline fen, $N = 9$; *Molinia* wet meadow, $N = 3$; and dry meadow, $N = 6$; Figure S1). The number of points per habitat type were proportional to the habitat surface in the restored areas. Four additional sampling points, one for each habitat type, were placed in the adjoining natural vegetation (not restored) as target vegetation, considered representative in terms of soil moisture and species composition (Appendix S1). At each point, a permanent plot of $4\,m^2$ ($2 \times 2\,m$) was established during the first year after restoration. Vegetation surveys were conducted in 2007, 2008, 2009, 2010, 2011 and 2020 for most of the plots. During the surveys, the occurrence and the estimated cover value (% of plant cover compared to plot area) of all vascular plants were recorded in each plot.

Overall, 85 vegetation surveys were conducted: 21 in *Cladium* fens, 34 in low alkaline fens, 12 in *Molinia* wet meadows and 18 in dry meadows (Table S1). The oldest plot was 21 years old (recorded in 2020 and restored in 1999), while the youngest plot was 1 year old (recorded in 2011 and restored in 2011).

Species nomenclature followed Poldini et al. (2002), exotic status was assigned considering both neophytes (i.e. plants introduced after 1500), according to Buccheri et al. (2019) and archaeophytes (i.e. plants introduced before 1500), according to Poldini et al. (2002). Plant life-span was considered by classifying the species in annuals vs perennial. Functional changes across time were analysed selecting two leaf traits considered as dependent on community structure changes, namely leaf area (size LA) and leaf dry matter content (LDMC) (Pérez-Harguindeguy et al., 2013). We selected LA to represent the potential energy and water balance (Díaz et al., 2016) and photosynthesis (Dayrell et al., 2018), and LDMC to represent the resource acquisition capacity, water use, life span and stress tolerance (Dayrell et al., 2018; Díaz et al., 2016). Leaf functional trait data were derived from Kleyer et al. (2008) and were expected to describe changes in leaf functional traits of plant communities toward the reference vegetation for each habitat target

(Appendix S2). Environmental variability was indirectly assessed using plant Landolt's Indicator Values (Landolt et al., 2010), considering (i) nutrient indicator value and (ii) moisture indicator value (for details see Appendix S2).

Data collection and field work were conducted under the supervision and permission of the regional government of Friuli Venezia Giulia, owner of the sites.

2.4 | Data analysis

Preliminarily, mean values of all the considered functional traits, ecological indicators and species diversity indices were calculated for each plot in the considered year of survey (i.e. 85 plots; dataset available in Mosanghini et al., 2022). Species richness (number of species) and evenness (Pielou's index) were considered as alpha-diversity indices. Mean functional trait values were calculated as the arithmetic mean of the trait values of each recorded species (without weighing for abundance). The abundance was not used in this calculation to avoid the overweight of dominant species and to better describe the rapid changes in species composition occurring in restoration sites. Number of alien species and percentage of annual species were also calculated. All the analyses were performed in R 4.0.5 (R Core Team, 2021).

2.4.1 | Alpha-diversity and functional traits

The relationships between the considered vegetation indices and age since restoration (years) and its interaction with habitat type (i.e. waterlogging gradient) were tested by using linear mixed-effects models (LMM; $p < 0.05$). LMM were applied including the plot id as random factor and the AR(1) term for temporal autocorrelation. LMM were applied using the 'NLME' package. We manually removed interaction terms from final models when p-values were higher than 0.05 (full models in Table S4). Spatial autocorrelation was assessed calculating Moran's I values at distance classes, no evidence for spatial autocorrelation was detected (p-value > 0.05). Assumptions of models were verified using the diagnostic plots of model residuals. Where model residuals violated any linear model assumption, variables were log-transformed. Pairwise comparisons were performed using the 'emmeans' function within the 'EMMEANS' package R package. Slopes of significant interactions between the considered variable and the stage of restoration were further pairwise compared using the 'emtrends' function of the same package.

2.4.2 | Beta-diversity and floristic distance to target vegetation

The changes of plant species composition over time of succession (years since the restoration action) were assessed using the overall and partitioning beta-diversity indices of turnover and nestedness (Baselga, 2010). Beta-diversity indices were calculated using the

'beta.pair' function of the 'BETAPART' package, based on the Jaccard index. The analyses of changes over time were performed by regression on distance matrices (MRM) (Lichstein, 2007). The response matrices were the considered beta-diversity dissimilarity indices (i.e. overall beta-diversity, turnover, nestedness), the explanatory matrix was the restoration age distance (years) between each pair of plots. MRMs were conducted separately for each response variable, using a linear model with and without a quadratic term to account for possible nonlinear relationships. Statistical significance was determined using permutation tests ($n = 9999$). The MRM analyses were conducted using the 'ECODIST' package. R^2 values were used to determine the variance explained by the model.

We further explored the relationships between age of restoration and species composition resemblance with target vegetation. For all the plots, the differences in plant species composition to target vegetation plots were assessed using the overall and partitioning beta-diversity indices of turnover and nestedness. The relationships between species composition distance and age since restoration (years) and its interaction with habitat type (i.e. waterlogging gradient) were tested by LMM ($p < 0.05$). LMM were applied including the plot id as random factor and the AR(1) term for temporal autocorrelation. We removed interaction terms from final models if p-values were higher than 0.05 (Table S5). Spatial autocorrelation, assumptions of models and pairwise comparisons were performed using the same approaches applied to alpha-diversity indices.

3 | RESULTS

3.1 | Changes in plant diversity and functional traits

In total, 202 plant species were recorded during the surveys. On average, we found 17 species per plot. *Cladium* fens presented the lowest values (13), while the highest values were found in dry meadows (25). Changes in plant diversity are summarized in Figure 2.

Species richness significantly changed during the succession showing contrasting trends in the considered habitat types (Table 1; $R^2 = 0.30$). Species richness decreased moving toward the mature stages of *Cladium* fens, while it increased in the other communities with similar slopes ($p > 0.05$). The trajectories moved toward the number of species recorded in the target vegetation plots except for low alkaline fens, which slightly deviates from the target number (Figure 3a dashed lines). Similarly, Pielou's evenness index changed over time with a significant interaction with community type (Table 1, $R^2 = 0.40$). In this case, both *Cladium* and low alkaline fens showed negative trends, oppositely to *Molina* and dry meadows (Figure 3b).

Number of alien species rapidly decreased across the successional stages independently to habitat type, which presented different alien species richness ($p < 0.05$; $R^2 = 0.28$): lower in fens, intermediate in wet meadows and significantly higher in dry meadows (Table 1, Figure S2). Similarly, annual species showed a negative

trend moving toward the mature stages of restoration with not significant differences between plant communities (Table 1, Figure S2; $R^2 = 0.17$).

Considering the ecological indicators values, nutrient indicator value significantly changed during succession with a significant interaction with community type (Table 1; $R^2 = 0.83$). It rapidly increased in *Cladium* fens while it decreased in the other habitats, with similar slopes ($p > 0.05$). The trajectories moved toward the target vegetation value, except for low alkaline fens (Figure S3). Soil moisture indicator value was affected by habitat type, showing significant lower values in dry meadows, when compared to other communities (Table 1, Figure S3, $R^2 = 0.56$).

The analysed mean community LA presented a significant interaction between age since restoration and habitat type (Table 1, $R^2 = 0.50$). Leaf area increases over time in dry meadows and decreased in wet habitats, with similar slopes ($p > 0.05$). Trajectories of most plant communities diverged from the target vegetation value during succession (Figure S4). The mean community LDMC became higher moving toward the mature stages of restoration, with similar trends between habitats, which presented different mean values (Table 1, $R^2 = 0.46$). LDMC was significantly lower in meadows respect to low alkaline fens (Figure S4).

3.2 | Changes in species composition and floristic distance to target vegetation

For all the restored areas, we found a significant increase of the overall beta-diversity and turnover in pair of plots with high age difference. Instead, nestedness was higher in plot with similar age and decreased with the increase of age difference. Consistent trends were found for low alkaline fens habitat while wet meadows and dry meadows changes of beta-diversity were mainly due to species turnover. *Cladium* fens did not show any significant change in beta-diversity over time (Table 2).

We found that the overall beta-diversity between each plot and target plot decreased in old-restored plots of all considered habitats except for *Molinia*-meadows (Table 3, Figure 2c; $R^2 = 0.58$), where it was higher and constant. Beta-diversity turnover and nestedness between each plot and target plot was affected by time since restoration and habitat type but not by their interaction (Table 3). Beta-diversity turnover ($R^2 = 0.42$) decreased over time since restoration, and it was significantly higher ($p < 0.05$) in low alkaline fens than in *Cladium* fens and dry meadows (Figure S4). In contrast, beta-diversity nestedness increased toward old stages of succession ($R^2 = 0.32$) and it was significantly higher in *Cladium* fens than low alkaline fens and wet meadows (Figure S4).

4 | DISCUSSION

The succession following the restoration actions evidenced different trajectories in plant diversity for the considered habitats, mainly
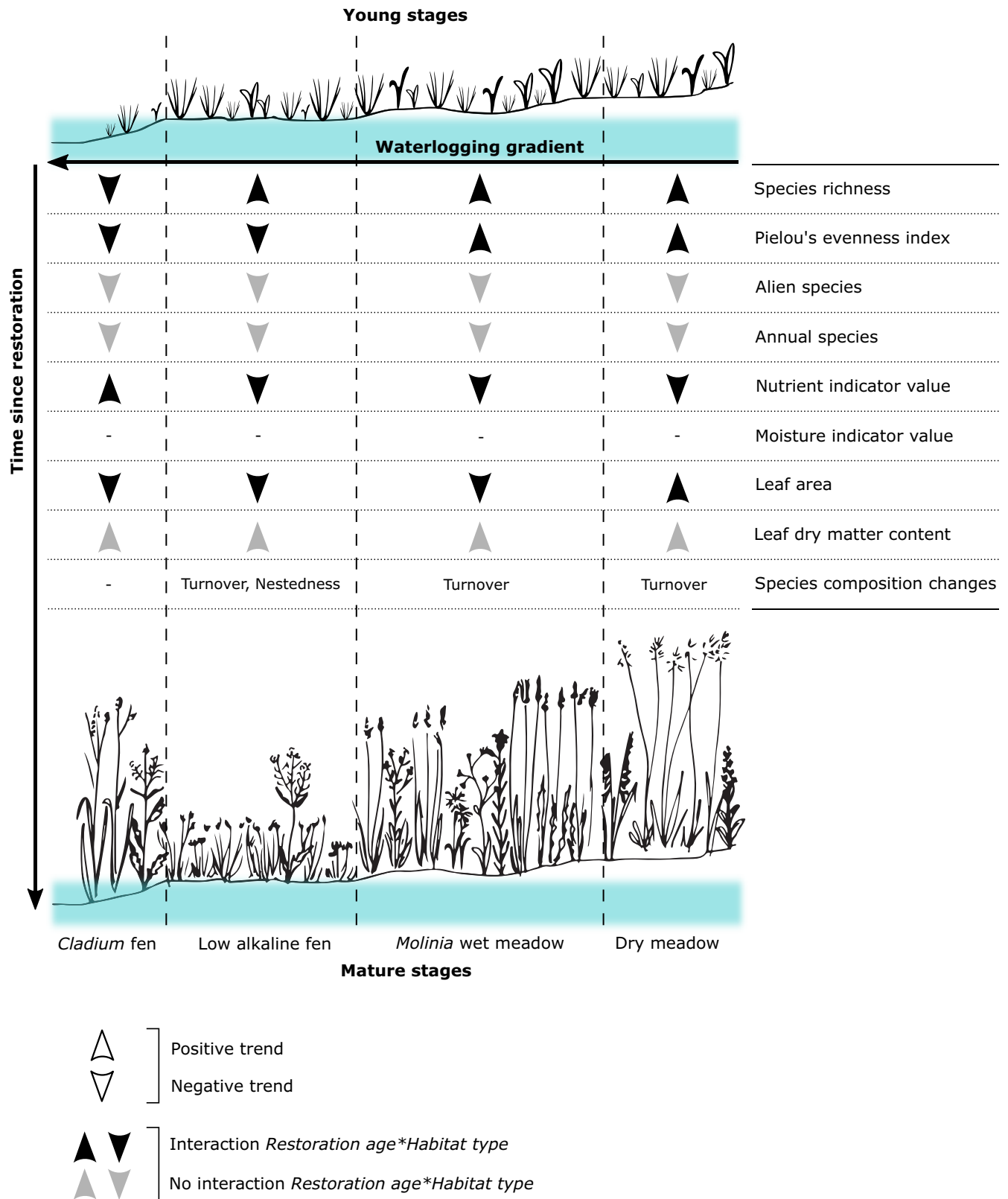
FIGURE 2 Graphical summary of the significant changes occurred across the plant successional stages (time since restoration) and the waterlogging gradient for the analysed indices of biodiversity, plant traits and species composition.

tending toward the values of vegetation references. Plant diversity decreased in old-restored areas of wet habitats while it increased in dry sites. As expected, we found a decrease of exotic and annual species across the successional stages (but this was not affected by waterlogging) and changes of community leaf trait syndrome toward mature stages.

TABLE 1 Effects of restoration age, habitat type and their interactions on diversity indices and selected plant traits. Values are estimated from final LMMs. Interactions were removed when p-values > 0.05, in bold significant values. Degrees of fredom (df), Fisher value (F-value) and p-values are shown

Model	Variable	df	F-value	p-value
Species richness	Restoration age	1–54	0.968	0.3295
	Habitat type	3–19	4.495	**0.0152**
	Restoration age × Habitat type	3–54	4.314	**0.0085**
Pielou's evenness index	Restoration age	1–54	7.244	**0.0094**
	Habitat type	3–19	3.387	**0.0395**
	Restoration age × Habitat type	3–54	4.675	**0.0056**
Alien species	Restoration age	1–57	13.782	**0.0005**
	Habitat type	3–19	4.322	**0.0175**
Annual species	Restoration age	1–56	15.483	**0.0002**
Nutrient indicator value	Restoration age	1–49	0.770	0.3844
	Habitat type	3–19	1.628	0.2162
	Restoration age × Habitat type	3–49	7.179	**0.0004**
Moisture indicator value	Habitat type	3–19	13.945	**<0.0001**
Leaf area	Restoration age	1–54	5.819	**0.0193**
	Habitat type	3–19	1.957	0.1548
	Restoration age × Habitat type	3–54	3.578	**0.0196**
Leaf dry matter content	Restoration age	1–57	38.276	**<0.0001**
	Habitat type	3–19	6.371	**0.0036**

In old-restored plots the composition distance to target vegetation generally decreased over time, showing contrasting responses for species turnover and nestedness. Our findings suggest that waterlogging stress strongly shaped successional community changes, acting as main abiotic filter. This filter seemed to be stronger at the extreme points of the gradient, generating opposite but faster dynamics than at intermediate conditions.

4.1 | Diversity and functional trends

Changes in species richness along the ecological successions not always showed consistent trajectories (Wali, 1999; Wiegleb & Felinks, 2001). In our study, the observed contrasting trends could be due to the waterlogging effects. Acting on similar species-rich pioneer plant communities, the waterlogging increased the differences between sites over time (years since restoration) according to its intensity and duration. More specifically, plant diversity was sensitively higher than in reference sites for the habitat more subjected to flooding, as found also in other studies (Balcombe et al., 2005; Gutrich et al., 2009), while it remained constant or increased across the successional stages at intermediate waterlogging or in dry conditions, respectively. These dynamics suggest that the progression of species richness toward the target values of wet habitats appeared to be driven by the loss of early successional species rather than by a gain of species typical of high integrity wetlands (Matthews & Endress, 2008). In meadows, in contrast, the highest species diversity was found in old-restored areas, where species richness

was sometimes higher than in target vegetation (e.g. Balcombe et al., 2005; Campbell et al., 2002).

Two plant groups seemed to mainly elucidate the observed plant diversity trends, namely annual and alien species. Both alien and annual plants decreased across time since restoration, independently to waterlogging. Other studies demonstrated that in restored sites the number of alien and annual plants rapidly declines, reaching the equivalency to natural sites within 10 years (Boscutti et al., 2016; Gutrich et al., 2009). This has been linked to a sudden decline in germination rate of these groups (Perry & Galatowitsch, 2003). Moreover, ruderal plants suffered more in flooded areas, as response to the lack of traits for moisture tolerance (Richards et al., 2020). In addition, alien species were found to be more common in dry grassland, confirming the sensitivity of these habitat to invasion as response to soil and landscape disturbances (Boscutti, Sigura, et al., 2018; Geppert et al., 2021). It is also plausible that the high diversity values found at the early stages of the succession might be sustained also by to the use of native seeds during restoration (Boscutti et al., 2016; Farrell et al., 2021).

We found nutrients indicator value of plant communities to decrease (except for *Cladium* fens) across the successional stages, which might reflect changes in soil proprieties over time. For instance, the accumulation of soil organic matter can shape the capacity of water retention, also in dry soils. Soil proprieties might strongly interplay with other abiotic and biotic filters across the successional stages (Catano et al., 2021), generating important plant–soil feedbacks able to affect the ultimate properties and functions of plant communities (Boscutti et al., 2020; Pellegrini et al., 2018).
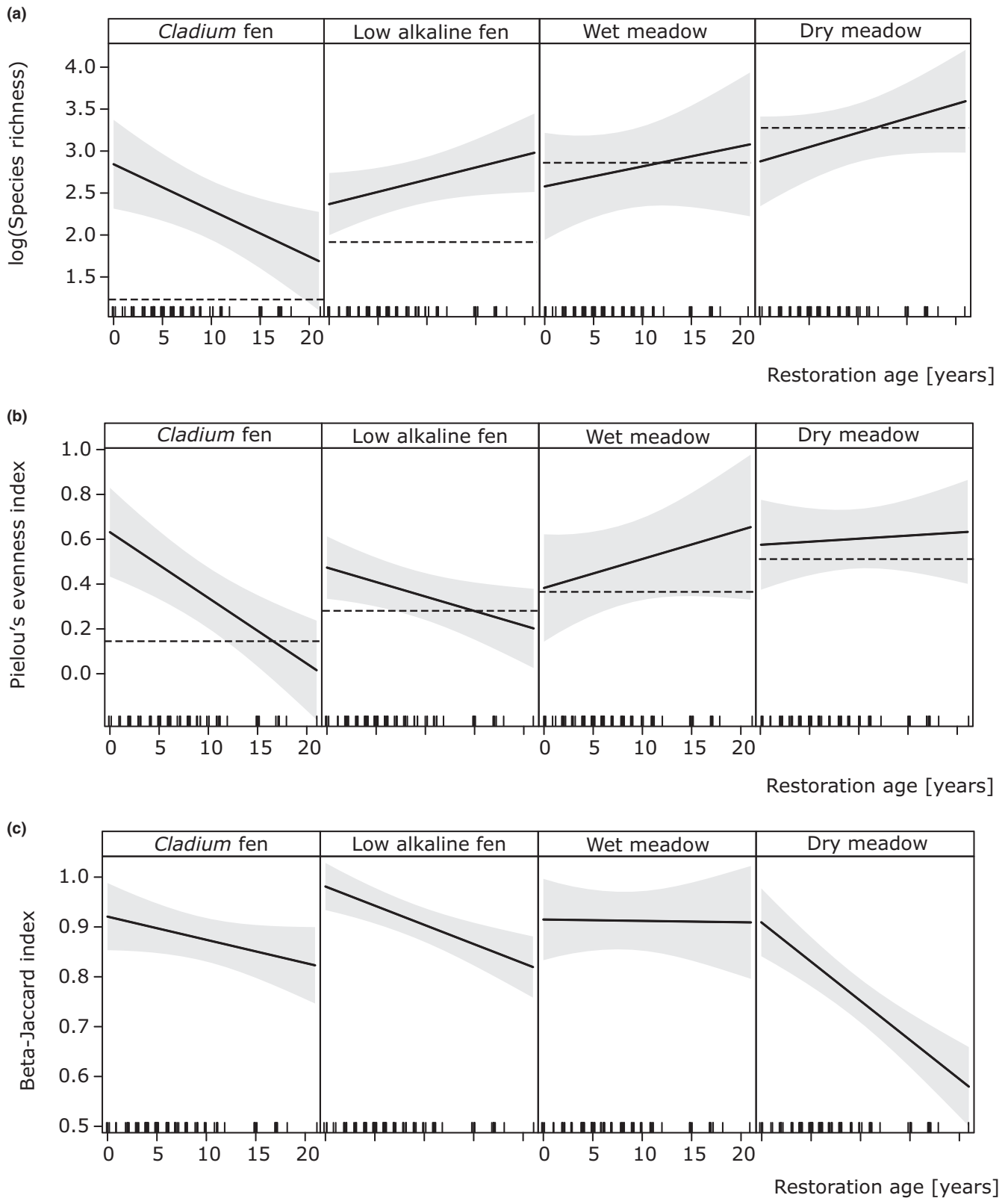
FIGURE 3 Effect plots of the interaction between restoration age and habitat type on (a) species richness, (b) Pielou's evenness index, and (c) floristic distance between each plot and target plot assessed using beta-Jaccard index. Dashed lines indicate values measured in the vegetation reference plots. Confidence intervals (95%) are shown.

We found the mean LDMC of the community to increase in old-restored stands, showing higher values in habitat more prone to flooding and a general decrease of LA (except for dry meadows).

Mature stages of restoration favour a leaf species syndrome of small leaves with low water content. These traits are typical of most of the dominant species of wetland communities, mainly belonging to the

TABLE 2 Changes of plant species composition across age of succession in terms of overall (beta-Jaccard index) and partitioning beta-diversity indices of turnover and nestedness in four target plant communities. R^2 values show the variance explained by the model. Only significant models are shown ($p < 0.05$)

	Beta-Jaccard index		Beta-turnover index		Beta-nestedness index	
	Slope	R^2	Slope	R^2	Slope	R^2
Total restored areas						
Linear	1.403	0.056	2.234	0.054	−0.830	0.021
Quadratic	−0.302		−0.592		0.290	
Cladium fen						
Linear	—	—	—	—	—	—
Quadratic	—		—		—	
Low alkaline fen						
Linear	0.775	0.088	1.362	0.093	−0.587	0.047
Quadratic	−0.175		−0.284		0.109	
Molinia wet meadow						
Linear	—	—	0.013	0.080	—	—
Quadratic	—		—		—	
Dry meadow						
Linear	0.821	0.290	0.921	0.275	—	—
Quadratic	−0.338		−0.421		—	

TABLE 3 Effects of restoration age, habitat type and their interactions on floristic distance between each plot and target plot assessed using beta-diversity indices. Values are estimated from final LMMs. Interactions were removed if p-values > 0.05, in bold significant values. Degrees of fredom (df), Fisher value (*F*-value) and p-values are shown

Model	Variable	df	*F*-value	*p*-value
Beta-Jaccard index	Restoration age	1–54	37.842	**<0.0001**
	Habitat type	3–19	10.318	**0.0003**
	Restoration age × Habitat type	3–54	4.368	**0.0080**
Beta-turnover index	Restoration age	1–56	22.496	**<0.0001**
	Habitat type	3–19	5.498	**0.0068**
Beta-nestedness index	Restoration age	1–57	7.990	**0.0065**
	Habitat type	3–18	4.678	**0.0138**

Poaceae and Cyperaceae families. Similar results have also emerged in other studies conducted on restored peat bogs, for example by Carvalho et al. (2019). Moreover, Dawson et al. (2017) found that in restored alluvial floodplain meadows, species with higher specific leaf area showed a legacy with the former agricultural land use duration. Consistently, Konings et al. (2018) observed that in restored wetlands a low nitrogen availability reduced the specific leaf area while increasing LDMC. The increase in LDMC observed in our study therefore might supports the observed decrease in nutrient indicator values over time. More specifically, it could be induced by a process in which slow growing species affect the ecosystem properties through leaf traits that keep nutrient mineralization low, hence reducing competition from faster growing species (Kazakou et al., 2006; Suter & Edwards, 2013). However, the shift in functional traits of plant community is often mediated by environmental stress (Boscutti, Casolo, et al., 2018; Pellegrini et al., 2018). Accordingly, we found waterlogging to shape the changes in LA across the successional stages, where the community LA decreased over time in flooded and wet habitats while increasing in dry meadows.

4.2 | Species composition and floristic distance to target vegetation trends

We found species composition changes to confirm that restoration seemed to be more effective at the extreme points of the gradient, generating opposite but faster dynamics than at intermediate conditions. This was better elucidated by changes in species turnover/nestedness rather than species diversity, as suggested by Balcombe et al. (2005) and Matthews and Spyreas (2010).

Previous studies demonstrated that harsh environmental features (e.g. soil waterlogging) constrained changes in community composition by increasing the strength of environmental filtering and affecting species competition (Budelsky & Galatowitsch, 2000; Catano et al., 2021).

Distance in species composition to target vegetation reduced over time due to a decrease of species turnover and an increase in nestedness. Il old-restored areas, hence, species composition mostly represent a subset of species found in natural wetlands, as also found in similar environments (Seabloom & van der Valk, 2003).

This trend was not consistent for all the studied communities suggesting that 20 years of restoration are perhaps not exhaustive to depict a comprehensive dynamic of wetland restoration (Matthews et al., 2009). Some observed divergences were probably linked to habitat waterlogging conditions, also due to a concurrent variation in trait composition (Catano et al., 2021).

Other studies highlighted that restoration outcomes strictly depended on site conditions, showing, for instance, a major convergence across resource-rich sites (Catano et al., 2021). In our sites trajectories of species assemblage where evident for harsh environment while wet meadows, with intermediate waterlogging conditions, showed uncertain and contrasting responses. In such conditions, it is plausible that other abiotic conditions (e.g. soil proprieties) still not met those of the target vegetation, generating a stagnation of species assemblages (Mclachlan & Knispel, 2005; Yabe et al., 2021). In addition, at intermediate conditions also trait-based filter are less effective favouring the persistence of the early-stage disturbance legacies (e.g. former land-use, landscape surroundings) affecting the community assembly (Laughlin et al., 2012).

4.3 | Implications for management and decision-making of wetland restoration

Our study has broad implications for the capacity of wetland restoration to recover and maintain biodiversity across time in the wetland mosaic generated by the waterlogging gradient. We here stress the importance to consider the waterlogging as main driver in generating contrasting trajectories of plant communities. In this context, while at the extreme point of the gradient the trajectories were contrasting and faster, accelerating the selection of species community consistent to target communities, at intermediate conditions the changes were slower and more uncertain. We thus suggest giving much effort to the management (i.e. mowing strategies and biomass removal) and further restoration action aimed at facilitating the ingression of some key species of these transitional communities (e.g. species transplantations, in-situ nursing). Moreover, we also demonstrated that creating steep environmental gradient in wetland restoration can promote broader conservation initiatives by reducing biotic homogenization and stabilizing ecosystem functions and services at landscape scale (Catano et al., 2020; Isbell et al., 2018).

We also found that plant trait syndrome moved toward mature stages, indicating for each habitat a specific plant community trait spectrum. This might provide some useful indications when applying restoration (e.g. seed mixture selection) and management practices (e.g. habitat specific) aimed at favouring some plant guilds instead of others (e.g. grasses and sedges vs dicot herbs), that could improve the achievement of a restoration stage consistent with surrounding target habitats.

Third, scaling-up restoration outcomes across waterlogging gradient and time should involve also other ecosystem processes, such as soil development. Plant–soil interactions can generate important feedbacks causing variation in species composition across restoration sites, enhancing the recovery of biodiversity at different scales.

All these perspectives might provide new tools for restoration science to advance global sustainability initiatives, in the 'Decade of Ecosystem Restoration', as proposed by the U.N. declaration for the 2020–2030.

AUTHOR CONTRIBUTIONS

All authors conceived the ideas and designed methodology; Giuseppe Oriolo has collected almost all the data, Davide Mosanghini and Francesco Boscutti collected the data in 2020; Davide Mosanghini and Francesco Boscutti analysed the data; Davide Mosanghini and Francesco Boscutti led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare that no competing interests exist.

DATA AVAILABILITY STATEMENT

Data available via the Mendeley Data https://doi.org/10.17632/dnvpcyp3fk.1 (Mosanghini et al., 2022).

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