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RESEARCH ARTICLE

Using functional traits and species diversity to evaluate restoration success of coastal dunes

Simon Chollet  | Françoise Rozé | Vincent Jung

CNRS UMR 6553 ECOBIO, Université de Rennes 1, Rennes, France

Correspondence

Simon Chollet, Université de Rennes 1, Rennes, France.

Email: simon.chollet@univ-rennes.fr

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Abstract

Questions: Evaluating reasons for the success (or failure) of restoration projects is one of the major goals for applied ecologists in the context of the dramatic worldwide decline in biodiversity. To that end, finding appropriate indicators and reference ecosystems is mandatory, especially for habitats in which restoration projects have been barely evaluated over the long term, such as coastal sand dunes. Do different indicators provide complementary information to evaluate restoration success? How successful is sand dune restoration after 30 years?

Location: Brittany (France).

Methods: We report changes in the plant community over a period of 30 years following restoration using trampling protection and marram grass (*Ammophila arenaria*) planting in four sites that were highly degraded by sand extraction and over-frequentation. We used several indicator types (geomorphological, taxonomic, functional) at different spatial scales (alpha, beta, gamma) to assess recovery since restoration in four sites of the northern coast of Brittany and undertook comparison with reference sites.

Results: Our results indicate that over the 30 years after restoration the gamma richness of typical species and overall vegetation conservation status increased. We also found that restoration induces the recovery of zonation in plant communities, which become organized along the typical sea-inland gradient. We showed that use of functional traits and diversity indices is effective to compare restored communities with reference data from the literature. Based on this approach, we demonstrated that, according to most functional indicators, restored communities converge over time with the patterns found in reference data.

Conclusions: We demonstrated that restoration of coastal dunes after 30 years induced the recovery of sand accumulation, typical species cover, sea-inland plant community zonation and community functional characteristics. Despite these positive results, which indicated overall success and confirmed interest in such restoration projects, we found an important discrepancy in restoration success among study sites (e.g., level of recovery of typical species cover, functional diversity). Finally, our study

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confirms the interest of functional composition and functional diversity as restoration success metrics.

KEYWORDS

coastal sand dune, community-weighted mean, functional diversity, functional trait framework, reference communities, restoration ecology, restoration success, vegetation conservation status

1 | INTRODUCTION

Because two-thirds of the earth's surface has already been degraded or converted to agriculture, evidence indicates that traditional conservation strategies based solely on the protection of the remaining natural habitats will not avoid mass species extinction, particularly in a world facing a still-growing human population and changing climate (Suding et al., 2015; Chazdon et al., 2017). Ecological restoration is increasingly seen as a complementary and necessary approach to avoid the worse consequences of human-induced loss of biodiversity (IPBES, 2018; Díaz et al., 2019). This evidence has led international institutions to adopt a resolution announcing that 2021–2030 is the United Nations Decade on Ecosystem Restoration (www.decadeonrestoration.org, <https://undocs.org/A/RES/73/284>).

Although the experiences of the past three decades have greatly improved our capacity to restore ecosystems, numerous challenges persist (Perring et al., 2015) including the evaluation of restoration success, which although identified as essential early on, remains one of the most important challenges (Benayas et al., 2009; Wortley et al., 2013; Evju et al., 2020). Evaluating restoration success is crucial in order to inform stakeholders, develop best practice guidelines or adjust restoration activities when projects do not follow the desired trajectories (Evju et al., 2020). Difficulties in evaluating restoration success are linked to the choice of pertinent indicators (see, for example, the debate between Reid (2015) and Suganuma & Durigan, 2015) and the availability of reference ecosystems with the same ecological and biogeographical conditions as the restored ecosystems (Török & Helm, 2017). The use of functional indicators based on species traits has repeatedly been proposed to improve the evaluation of restoration success (Cadotte et al., 2011; Engst et al., 2016; Carlucci et al., 2020). These indicators may avoid pitfalls due to the selection of target species and offer the possibility of diagnosing the reason for a failed restoration (Török & Helm, 2017; Evju et al., 2020). Despite high levels of interest, the use of functional traits for restoration still needs to be expanded (Török & Helm, 2017; Wainwright et al., 2018; Evju et al., 2020).

Although distributed across almost all latitudes and accounting for nearly one-half of the world's ice-free coastline, coastal dune systems are restricted in their inland extension and consequently cover only a small area worldwide; however, they host a highly specialized biodiversity of great conservation interest (Van Der Maarel, 2003; Martínez et al., 2004; Maun, 2009). These ecosystems are characterized by a strong sea-inland abiotic gradient that is responsible for the large heterogeneity and specialization of plant

and animal communities (Acosta et al., 2008; Conti et al., 2017; Torca et al., 2019). Natural disturbances (sand burial due to instability of the substrate) and stresses (salt spray, water deficit and nutrient availability) are related to the spatial organization of plant communities (Maun, 2009; Ciccarelli, 2015). As a consequence, in European dune systems it is usually possible to recognize the following typical sea-inland zonation: annual vegetation of drift lines (EUNIS habitat classification: N112); embryonic dunes (=pioneer dunes, EUNIS habitat classification: N131); shifting dunes (=white dunes, EUNIS habitat classification: N133); and fixed coastal dunes (=grey dunes, EUNIS habitat classification: N151). From a human perspective, sand dunes provide numerous functions important for well-being, such as coastal protection against flooding or major recreational areas (Barbier, 2015; Morris et al., 2018; Drius et al., 2019). However, and despite their above-mentioned importance, sandy coastal environments and sand dunes in particular are currently recognized as among the most threatened ecosystems worldwide (Feagin et al., 2005; Schlacher et al., 2007; Provoost et al., 2011; Defeo et al., 2021). In Europe, for example, since the beginning of the 20th century, 70% of these habitats have been highly degraded (Brown & McLachlan, 2002; McLachlan & Defeo, 2017). Anthropogenic threats to these habitats are numerous and depend on the location and configuration of the sand dunes, but usually include sea-level rise, urbanization, nitrogen deposition, (exotic) tree plantations, and an excessive and unordered influx of people (Marchante et al., 2008; Defeo et al., 2009; Doody, 2012; Fantinato, 2019). To improve the conservation status of these important habitats for biodiversity conservation and the ecological services they provide, numerous projects aiming at restoring degraded sand dune ecosystems have been implemented over the past 40 years (Lithgow et al., 2013; Martínez et al., 2013; Feagin et al., 2015; Sutton-Grier et al., 2015). These restoration projects usually involve the re-accumulation of sand through the installation of passive sand-trapping systems, and often also include plantations of species known as "dune builders" (i.e., *Ammophila arenaria*, *A. breviligulata*, *Elymus farctus* and *Panicum amarum* depending on the region considered; Fischman et al., 2019). Despite numerous projects around the world, few long-term studies have evaluated the success of dune habitat restoration, particular their biodiversity value (Lithgow et al., 2013; Della Bella et al., 2021).

The main goal of our study is to evaluate the success of 30 years of dune restoration based on marram grass (*Ammophila arenaria* subsp. *arenaria*) plantation and trampling protection in four dune sites in Brittany (France). Marram grass planting is a common strategy known to increase sand accumulation and dune stabilization

(Hobbs et al., 1983). However, evaluating restoration success in sand dune habitats presents several challenges because these habitats are highly dynamic and their plant communities are spatially organized. In addition, no well-conserved local dune communities that could be used as a reference for plant species composition and functioning usually exist owing to the above-mentioned extensive degradation, challenging the definition of restoration success (Lithgow et al., 2013). To evaluate restoration success we used three complementary approaches. First, we used the classical increase in typical compared with non-typical species as an indicator of restoration success. Typical species could be defined as the plant species expected in the absence of habitat degradation, which corresponds to habitat-specialist species, but also includes often co-occurring generalist species as well as rare species (Jung et al., 2021). Second, because sand dune communities are distributed along the sea-inland gradient, we used the spatial distribution of β -diversity as an indicator of restoration success. Third, we analysed relevant functional traits to confirm that restored plant communities show the same functional characteristics as reference communities (using data from the literature because no well-preserved communities exist in Brittany). We used this functional approach because of a lack of reference communities near the study site that are comparable in terms of species composition. Thus, we consider restoration to be successful if: (1) the abundance of typical species increases after restoration, but the abundance of non-typical species does not; (2) species β -diversity increases with the distance between vegetation samples along the sea-inland gradient, indicating a restored spatial distribution; (3) restored communities have the same functional trait patterns along the sea-inland gradient as the reference communities.

2 | METHODS

2.1 | Study sites and sampling

On sandy coastal dunes several plant communities are spatially organized along the sea-inland gradient. On the French Atlantic coast the first occurring habitat, middle European sand beach annual communities (EUNIS habitat classification review 2021: N112, Habitat directive Annex I: 1210), is strongly influenced by salt spray and the high level of nutrients provided by the drift line, and is characterized by the presence of annual halo-nitrophilous species. Contiguous to this habitat are embryonic dunes (EUNIS habitat classification review 2021: N131, Habitat directive Annex I: 2110) that are reached by salt water only during very high tide and are characterized by species able to handle the high mobility of the substrate. The third habitat, a shifting dune with *Ammophila arenaria* (EUNIS habitat classification review 2021: N133, Habitat directive Annex I: 2120), is usually located on the more dynamic part of the dune system. Sand accretion on the shifting dune leads to the formation of a foredune ridge, thus protecting the backdune and allowing development of the last habitat in the gradient: the fixed grey dune (EUNIS habitat classification review 2021: N151, Habitat directive Annex I: 2130). Our

study took place at four sites located along 20 km of the northeast Brittany coast (48°41'N, 1°57'W; Appendix S1). The area is characterized by a temperate oceanic climate with mild summers (average temperature: 17.3°C) and cool winters (average temperature: 7.3°C); precipitation (average: 984 mm) is relatively evenly distributed across the seasons (average 1981–2010, Météo France). In this part of Brittany most of the coast is rocky and sand dunes make up only little pocket beaches of small size (Guilcher & Hallégouët, 1991). All the studied dunes are of similar late Holocene origin (following Wisconsinian regression) and composed of the same sandy materials (Guilcher & Hallégouët, 1991). The four sites are located in protected areas ("Conservatoire du littoral"), but differ in size, inland maximum extension, sea exposure and landscape context (e.g. Hue site is located in a dense urban context, whereas the other three are not; Appendices S1 and S2). Before restoration, all the sites were strongly disturbed by human activity (sand extraction, uncontrolled tourism), dramatically reducing the dunes' sand stock. Vegetation was very scarce and only few species were present (Figure 1; personal observation of F.R.); this was particularly the case at the Verger site owing to use of the dune as a wild parking place soon before the restoration project began. Because the study sites are the main dune sites in the area and all were previously degraded, no obvious difference in distance to propagule sources could be inferred at the onset of the study. The same restoration strategies were used at all sites (see Rozé & Lemauiel, 2004 for details). In April 1988, the local council (Ille-et-Vilaine Department) installed wooden fences to prevent trampling and planted marram grass (*Ammophila arenaria* subsp. *arenaria*) to promote sand accumulation (Rozé & Lemauiel, 2004).

2.2 | Geomorphology and vegetation sampling

Geomorphology and vegetation were surveyed at four dates following restoration: 1989 (1 year after restoration), 1998, 2011 and 2019 (31 years after restoration). Depending on site size, both vegetation and geomorphology were surveyed along two or three permanent transect lines (Appendix S2). Transects were placed perpendicular to the dune in order to be representative of the sea-inland gradient and offer the possibility of documenting recovery of the topographic profile (formation of a foredune ridge) and the different plant communities (drift line, embryonic, shifting and fixed dunes). To document sand accumulation over time, topographic profiles were constructed from theodolite measurements taken along each transect line in 1989 and 1998. In 2010 and 2019, measurements were undertaken using another methodology (electronic total station) that provides a digital elevation model from which sand accumulation could be calculated. Because of the change in survey methodology, direct comparison is not possible and we consequently decided to compare the sand accumulation in two phases, first between 1989 and 1998, and second between 2010 and 2019. Vegetation was sampled along belt transects (Del Vecchio et al., 2019), which consist of contiguous 1 m × 1 m quadrats laid out in the direction of the environmental gradient (number of initial quadrats sample in 1989 per site: Chevret,

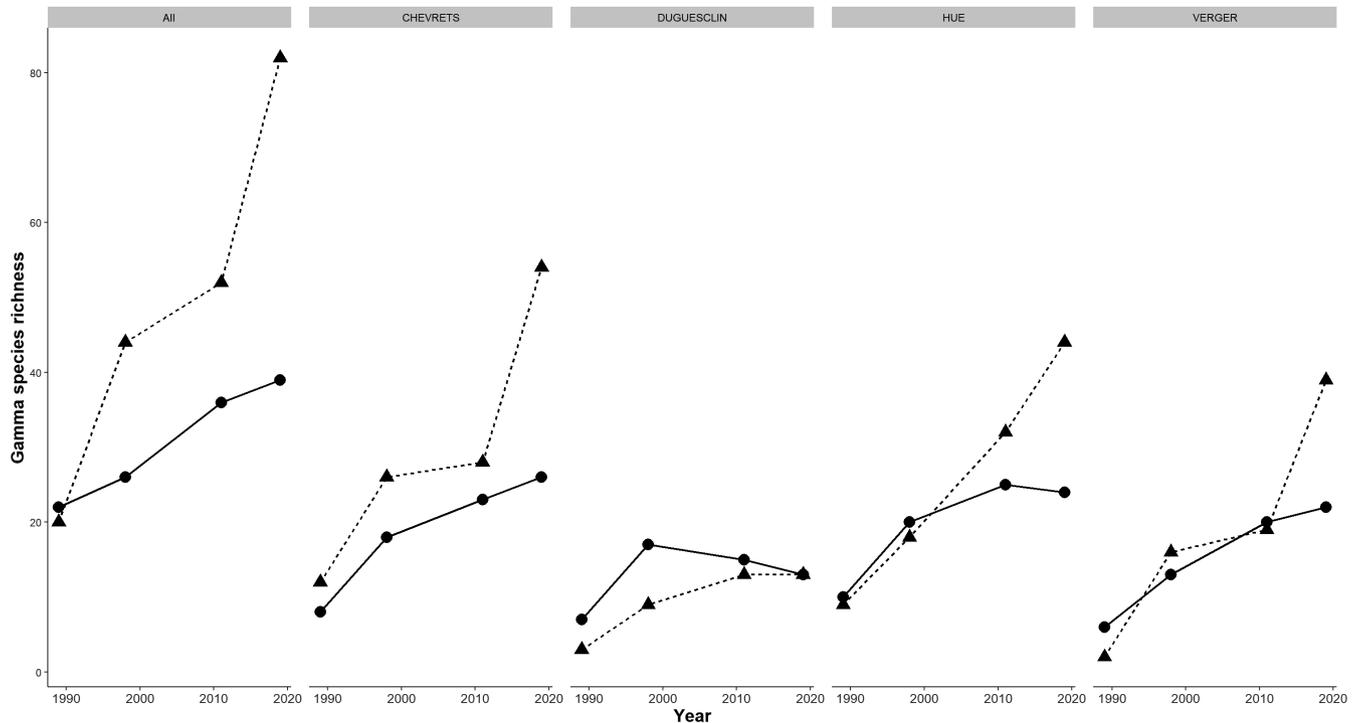


FIGURE 1 Change in gamma species richness over time after restoration in each site for typical species (black dot, solid line) and other species (black triangle, dashed line).

111; Du Guesclin, 58; Hue, 46; Verger, 80). Because of the extension of the vegetation after restoration, the transect size was increased throughout the study, leading to more quadrats being sampled in recent years (total number of quadrats sampled: 1989, 295; 1998, 314; 2011, 389; 2019, 410; Appendix S3). In each quadrat, every vascular plant species was identified and cover was estimated using the Braun-Blanquet scale. Bryophytes were not identified at the species level except for one typical species, *Tortula ruraliformis*. For other bryophytes only the total cover as a group was estimated.

2.3 | Reference communities and typical species

To evaluate restoration success we compared our restored dune communities with the vegetation in the reference communities. However, because all the sand dune sites in northern Brittany were strongly degraded by human activity, we chose references for the four communities (drift line, embryonic, shifting and fixed dunes) from the literature (see Appendix S4 for details). In each case, we used historical phytosociological relevés sampled along the Atlantic coast of France or Ireland which were originally used to describe each of the four studied communities. The chosen phytosociological associations were *Beto maritimae-Atriplicetum laciniatae* for drift line community (EUNIS habitat classification: N112), *Euphorbio paraliae-Elymetum boreoatlantici* for embryonic dune (EUNIS habitat classification: N131), *Euphorbio paraliae-Ammophiletum arenariae* for shifting dune (EUNIS habitat classification: N133) and *Hutchinsio petrae-Tortuletum ruraliformis* for fixed dune (EUNIS habitat

classification: N151). For each community between 9 and 19 phytosociological relevés including species composition and cover estimated by the Braun-Blanquet scale were used (see Appendix S4 for details concerning choice of references). To select typical species for each habitat in order to define typical species for the restoration we used the species mentioned in the description of the different dune habitats provide by the French interpretation manuals of European Union habitats (Bensettiti et al., 2002, Appendix S4).

2.4 | Statistical analyses

We analysed the change in typical cover of each species over time using a zero-inflated Generalized Linear Mixed Model (GLMM) (Brooks et al., 2017) with year as a fixed factor and site as a random factor. Zero-inflated GLMMs were used because of the large number of empty quadrats, particularly in the first years after restoration. To account for possible temporal dependences among the different surveys we used a first-order autoregressive model for the random errors. To evaluate restoration success we used the Vegetation Conservation Status (VCS) index (Jung et al., 2021) to assess global vegetation recovery. This recently developed index is based on the classical Simpson's diversity index, but uses the concept of species pools to integrate the influence of "typical" and "non-typical" species. The VCS index is maximized if there are many typical species with equally distributed abundances and if non-typical species are not abundant, and is calculated as: $VCS = \left[1 - \sum \left(\frac{n_j}{N_T} \right)^2 \right] \times \left(\frac{N_T}{N} \right)^2$ where n_j is the abundance of each typical species j , N_T is the sum of

the abundance of all typical species, and N is the sum of the abundance of all species including both typical and non-typical species. We classed species typical from other coastal habitats (e.g., sea-cliff communities) as neutral (i.e., neither typical nor non-typical), implying that they are not included in the calculation of the VCS index (Jung et al., 2021). All other species were considered non-typical and corresponded mainly to nitrophilous species, non-coastal ubiquitous species or non-native species (Table S4). We compared the VCS value calculated for each plot among years and sites using a two-way analysis of variance (ANOVA) and Tukey's post-hoc test of differences when models were significant.

We used β -diversity to evaluate restoration of the vegetation distribution along the sea-inland ecological gradient. We expected that successful restoration would conduce to an increase in dissimilarity between vegetation samples proportional to the spatial distance among quadrats. Consequently, we performed Non-metric (Distance) Multidimensional Scaling (NMDS) (Kruskal, 1964) which compared each quadrat pair using the Bray-Curtis index (i.e. a measurement of β -diversity including species abundance). We then tested the link existing between the first axis of the NMDS (reflecting gradient of vegetation composition) and the measured distance to the shore with a three-way analysis of covariance (ANCOVA) including spatial distance, site and year as explanatory variables.

Although reference data from literature may be highly valuable in evaluating restoration success, one big challenge is that these data were collected using another sampling protocol (plot size) and in another biogeographical context, limiting the possibility of direct comparison of, for example, species richness or typical species identity. To reduce these biases, we compared restored and reference dunes on the basis of their functional traits composition. Our expectation is that in the case of successful restoration, plant functional trait filtering along the sea-inland gradient should be similar to that found in the four types of reference communities, inducing a similar functional trait composition. To that end, we selected five plant characteristics known to vary along the sea-inland gradient (Conti et al., 2017; Torca et al., 2019). The first two traits were the Ellenberg indicator value of species for nutrient and salt tolerance. Second, we used two traits implied in the leaf economic spectrum (Wright et al., 2004), namely specific leaf area (SLA) and leaf dry-matter content (LDMC). In addition, we selected the seed mass, a trait linked to dispersion, persistence and the establishment success of species. We obtained the species traits data from different databases: BaseFlor (Julve, 1998) for the Ellenberg indicator value and LEDA (Kleyer et al., 2008) for SLA, LDMC and seed mass. For each trait we calculated the community-weighted mean (CWM; trait values weighted by species abundance). We also calculated the three components of functional diversity: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) (Mason et al., 2005). Functional richness represents the volume of the multivariate functional trait space occupied by a community, functional evenness is the regularity of the distribution of abundance in the volume, and functional divergence is the divergence in the distribution of abundance in the volume (Villéger et al., 2008). To calculate functional

diversity indices we standardized all plant trait values (standardized to mean 0 and unit variance) and we used a Gower dissimilarity matrix. For FEve and FDiv, we used the abundance weighted indices (based on the median % of the Braun-Blanquet scale). We first used a multivariate approach to examine whether the functional trait pattern in the sample plots along the sea-inland gradient is globally consistent with the trait differences between the four reference communities. We performed principal component analysis (PCA) on the CWM and functional diversity indices of the four reference communities, and projected onto the ordination the restored communities as supplementary individuals (not contributing to the axis). We then explored the link between the coordinate of each restored plot on Axis 1 and distance to the sea using a three-way ANCOVA including spatial distance, site and year as explanatory variables. We also explored the importance of each of the functional characteristics and functional diversity indices as an indicator of restoration. For reference sites, one-way ANOVA was performed to compare values among the reference plant communities (drift line, embryonic, shifting and fixed dunes) and Tukey's post-hoc test of differences was applied when the models were significant. For restored sites, models linking CWM or functional diversity index to spatial distance, site and year were performed with a three-way ANCOVA. In each case, linear or quadratic models were chosen, according to the pattern found in the reference communities (linear or bell-shaped).

All statistical analyses were performed in R (version 4.1.1; R Core Team, R Foundation for Statistical Computing, Vienna, AT) using the packages *betapart* (version 1.5.6) (Baselga et al., 2018), *FD* (Laliberté & Legendre, 2010) and *glmmTMB* (Brooks et al., 2017).

3 | RESULTS

After restoration, the average sand accumulation at the foredune ridge was 1.58m during the first decade (1989–1998) and 0.60m during the last decade (2010–2019; Appendix S5). Overall, over the years we observed 186 species, 33% of which are considered typical of sand dune habitats. Among these typical species, our results indicate that the cover of 36% increased significantly over time (Appendix S6). The global number of typical species (i.e. gamma richness) increased at all sites; however, the patterns were different with a monotonous increase at Chevret and Verger sites, but an increase before stagnation and a small decline at Du Guesclin and Hue sites respectively (Figure 1). For other species (i.e. non-typical and neutral species), the increase in gamma richness was monotonous in all sites but one (Du Guesclin; Figure 1).

We observed that the vegetation conservation status value (evaluated using the VCS index) increased significantly over the years after restoration, with the maximum value reached in 2011 and 2019 ($F = 54.2$, $p < 0.001$; Figure 2). We also found that the speed of these changes differed among sites, with Du Guesclin and Hue reaching their maximum VCS value in 1998, whereas for the other sites VCS continued to increase until 2011 or 2019 ($F = 9.9$, $p < 0.001$; Figure 2). The increase in the VCS index value was driven

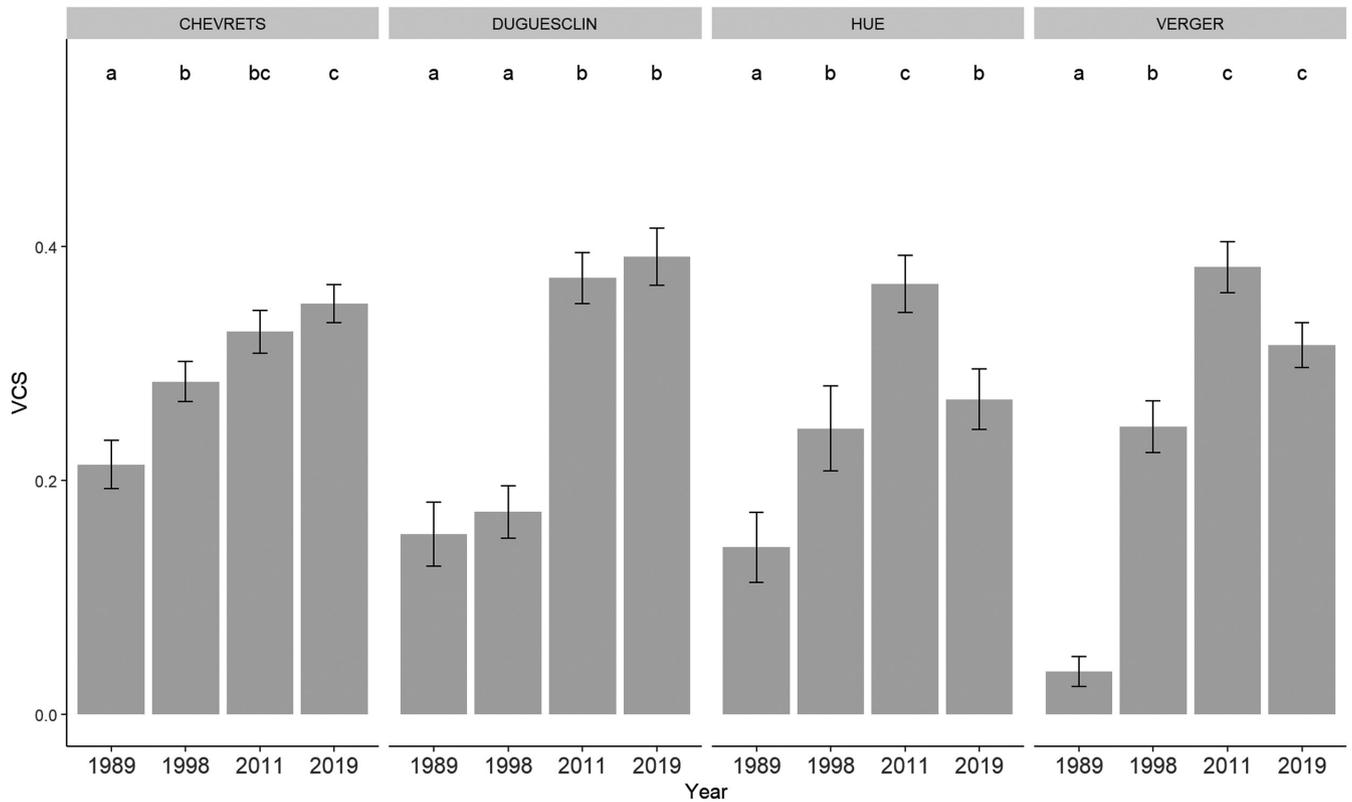


FIGURE 2 Change in Vegetation Conservation Status index over time after restoration in each site. Letters indicate significant differences according to Tukey's post-hoc tests.

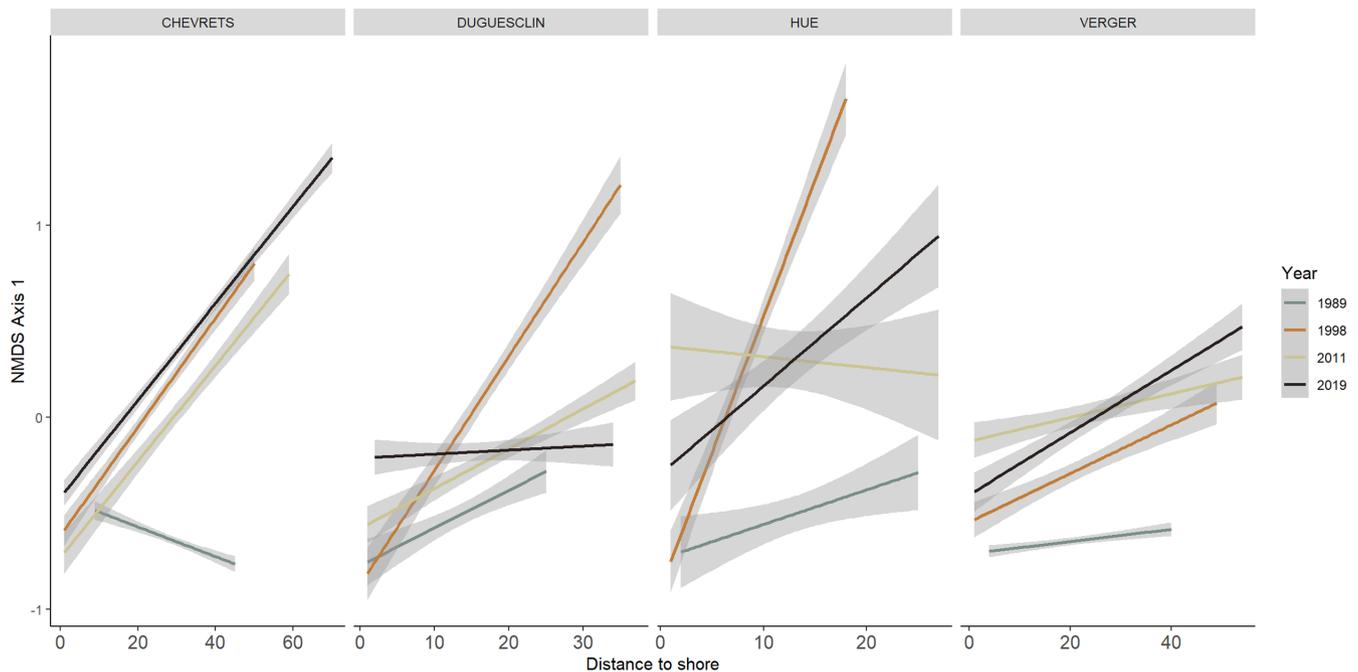


FIGURE 3 Relationship between spatial distance (distance to shore) and species composition distance (evaluated by Non-metric Multidimensional [Distance] Scaling ordination first axis).

mainly by an increase in the typical species richness (Appendix S7a). In recent years, the VCS index indicated a decline in the conservation status at one site, Hue, which was due to a strong increase in non-typical species richness (Appendix S7b).

Concerning restoration of the distribution of plant communities along the sea-inland gradient, we found that overall the relationship between vegetation composition (based on the first axis of an NMDS ordination) and spatial distance increases positively and became

stronger over time (i.e. two-way interaction between distance and year effects, $F = 64.5$, $p < 0.001$; Figure 3). One year after restoration (1989) the relationship between spatial and compositional distance was not significant, indicating an absence of the typical plant community organization along the sea-inland gradient ($F = 0.01$, $p > 0.05$; Figure 3, Appendix S8). From 10 years after restoration onwards we found a positive relationship between spatial and vegetation composition distance (Figure 3, Appendix S8). We also found that the change in the relationship between spatial and vegetation composition distance was different among sites (i.e. three-way interaction between distance, year and site effects, $F = 12.2$, $p < 0.001$; Figure 3). At the Verger and Chevret sites, the sea-inland distribution of the vegetation increased over time, but at Du Guesclin and Hue this relationship was variable among years (e.g. strong in 1998, but absent 2011; Figure 3).

We found that combination of the five functional traits and functional diversity indices allowed us to discriminate the four types of reference communities, with the first axis (49% of inertia) representing the sea-inland gradient (Figure 4a). Projection of the restored plots on this ordination indicates that a similar global functional pattern was found after 30 years (Figure 4b; $R^2 = 0.38$, $p < 0.0001$) but was absent 1 year after restoration (Figure 4b; $R^2 = 0.02$, $p > 0.05$).

In the sand dunes of the reference sites, we found that most trait CWM and functional diversity indices were different between the four types of dune (Figures 5 and 6). Along the sea-inland gradient we found a reduction in nutrient affinity, salt spray tolerance and seed mass, no clear tendency for SLA and functional evenness, and an increase in LDMC, functional richness and functional divergence (left-hand panels in Figures 5 and 6). In restored communities, the sea-inland gradient increasingly explained the distribution of the functional traits over time (Figures 5 and 6, interaction between year and distance variable, $p < 0.001$; Appendix S9). For nutrient affinity, we found that in two sites (Chevret and Verger) the plant communities were influenced by the sea-inland gradient in 2019; this was not the case in the two other sites, although it was already

the case 1 year after restoration in one site (Du Guesclin; Figure 5a). Concerning salt tolerance, plant communities were already organized as in the reference communities 1 year after restoration (higher salt tolerance closer to the sea shore) in two of the four sites and this tendency was confirmed 30 years after restoration in all but one site (Du Guesclin; Figure 5b). Concerning SLA, in 2019 and 1989, the pattern along the sea-inland gradient was globally similar in every restored sites, and comparable with that observed in the reference sites (Figure 5c). For LDMC, the found tendency was comparable with reference sites only in 2019, and not in 1989 (Figure 5d). In 2019, the pattern concerning seed mass was congruent with that in the reference dunes (however, the values remain much lower), but this was not the case in 1989 (Figure 5e). At every site, the functional richness and divergence patterns were closer to the reference in 2019 than they were the first year after restoration (Figure 6a,b). Concerning functional evenness, no clear patterns were found in the restored or reference communities (Figure 6c).

4 | DISCUSSION

4.1 | Positive effect of restoration on geomorphology, typical species and gamma species richness

As previously demonstrated elsewhere, we found that marram grass (*Ammophila arenaria*) plantation combined with trampling protection is a very efficient method allowing sand accretion and dune building (Lillis et al., 2004; Vestergaard, 2004; Grafals-Soto, 2012). Although the global outcome was positive, we found that sand accumulation mainly occurred in the first 10 years following restoration, with discrepancies among sites during the last decade. These differences were mainly due to winter storm erosion in the foredune, the newly formed dunes providing protection against winter storm flooding (e.g. Du Guesclin site, personal observation).

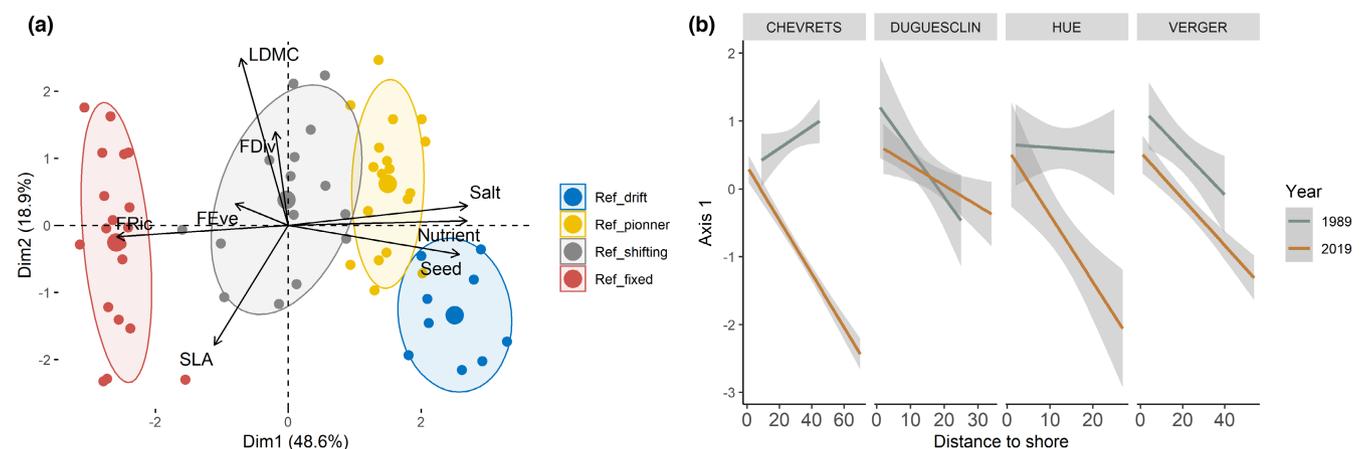


FIGURE 4 (a) Principal component analysis (PCA) on functional traits (SLA: specific leaf area; LDMC: leaf dry-matter content) and functional diversity indices (FRic, functional richness; FDiv, functional divergence; FEve, functional evenness) in reference communities. (b) Linear regression between the distance to the shore and the coordinates on Axis 1 of restored communities projected as supplementary points in the PCA of reference communities. To improve readability we represent only the first (1989) and last (2019) years of the study.

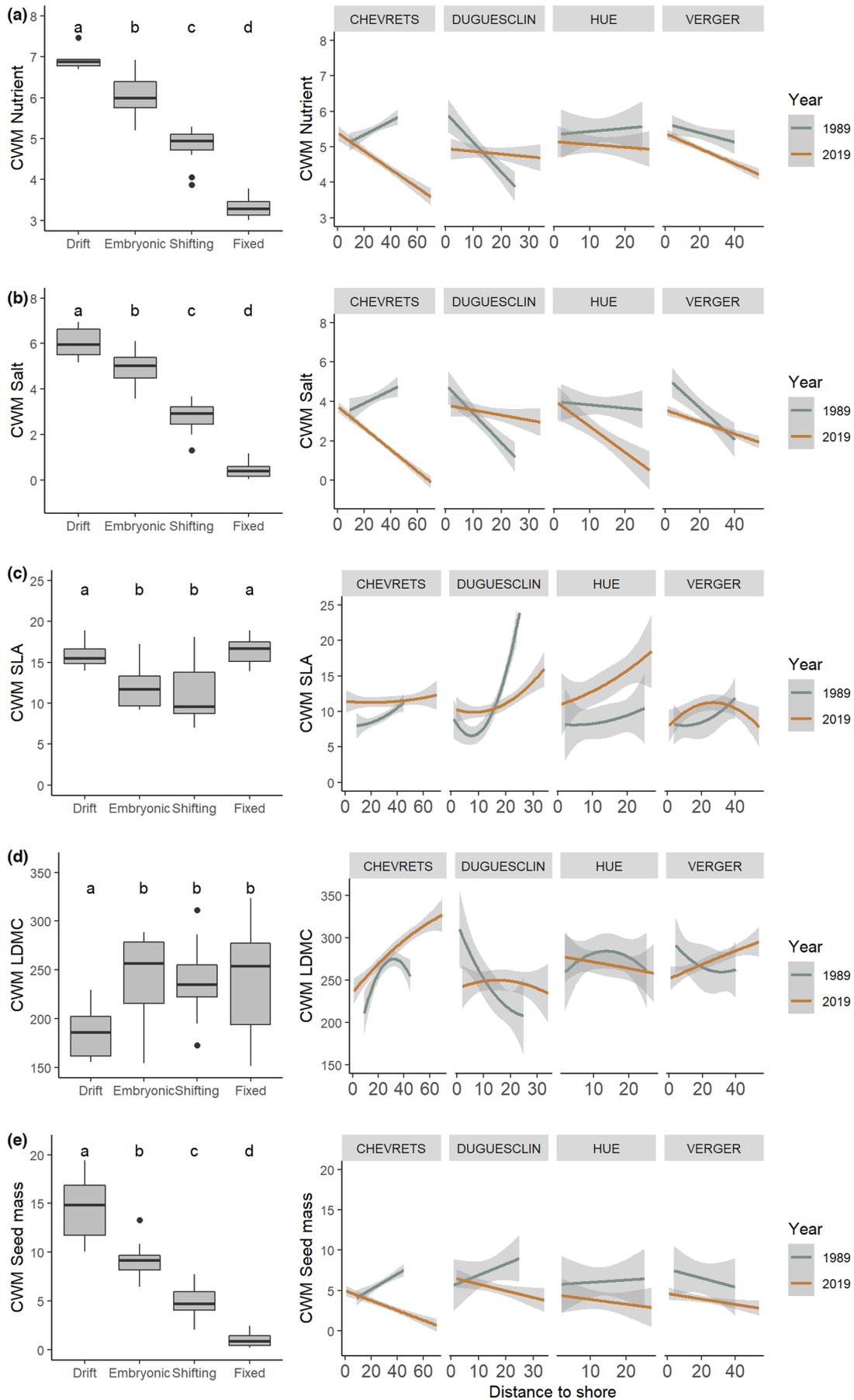


FIGURE 5 Community-weighted mean (CWM) in reference sites (left) and restored sites (right). For reference sites, analyses of variance were performed to compare the CWM value of each trait between reference communities. Letters indicate significant differences in the post-hoc Tukey's test. For restored sites, linear (salt, trophy, seed mass) and quadratic (specific leaf area [SLA] and leaf dry-matter content [LDMC]) models represent the link between CWM and distance to the shore (see Appendix S9 for model details). To improve readability we represent only the first (1989) and last (2019) years of the study.

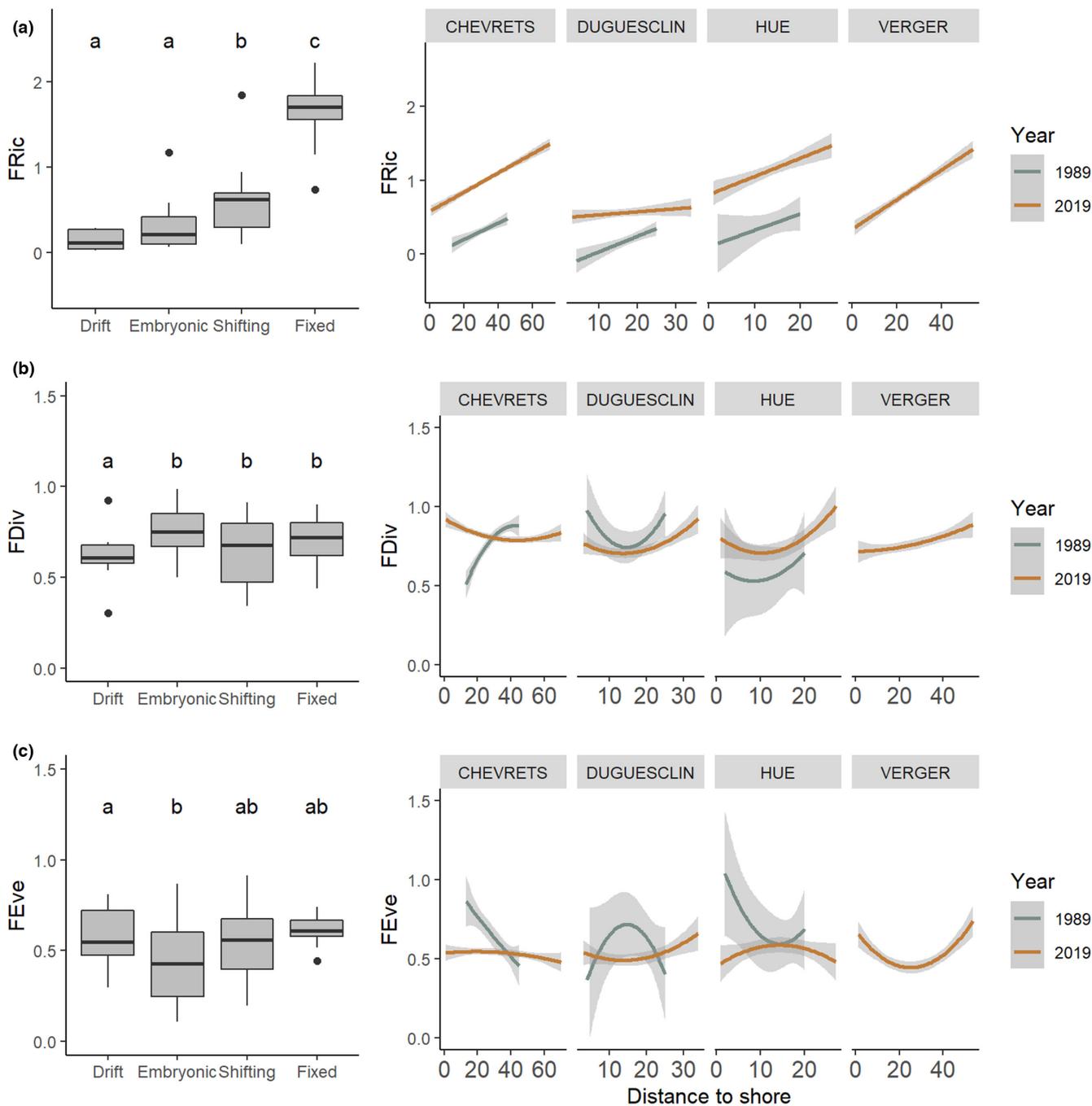


FIGURE 6 Functional diversity indices (functional richness [FRic], functional divergence [FDiv] and functional evenness [FEve]) in reference sites (left) and restored sites (right). For reference sites, analyses of variance were performed to compare the community-weighted mean (CWM) value of each index between reference communities. Letters indicate significant differences in the post-hoc Tukey's test. For restored sites, linear (functional richness [FRic]) and quadratic (functional divergence [FDiv] and functional evenness [FEve]) models represent the link between indices and distance to the shore (see Appendix S9 for model details). Because of the low number of species indices cannot be calculated for 1989 in the Verger site. To improve readability we represent only the first (1989) and last (2019) years of the study.

This positive effect of restoration on sand accumulation was followed by an increase in gamma species richness and by an increase in vegetation conservation status at the alpha (i.e. plot) scale. Restoration even promoted recovery of rare and regionally protected species such as *Eryngium maritimum*, which recolonized three of the four study sites. These results indicate that despite the isolation of the study sites, the restoration of sand dunes was not strongly limited by the colonization potential of typical species. Similar results have been found for the restoration of an isolated sand dune in Spain where most typical species also recolonized after restoration (Gallego-Fernández et al., 2011). Yet, the colonization deficit of typical species is often mentioned as an important limiting factor for a restoration project (Makoto & Wilson, 2019; Funk, 2021). We can explain the relatively low effect of this colonization deficit in sand dune restoration by the dispersion strategies of most of the species, which have long-distance dispersion capacities (Maun, 2009; Guja et al., 2010; Yang et al., 2012) and consequently are affected only marginally by habitat fragmentation (Malavasi et al., 2018).

4.2 | Vegetation conservation status, spatial distribution and functional traits as indicators of restoration success

It is well acknowledged that the choice of proper indicators is essential to evaluate restoration success (van Aarde et al., 1996; Ruiz-Jaen & Aide, 2005; Wortley et al., 2013; Török & Helm, 2017; Evju et al., 2020). Here, we suggest that the use of the VCS index (Jung et al., 2021) is particularly promising. This new metric was originally developed to compare the conservation value of communities, but we have shown that it could also be used to evaluate restoration success. In fact, by integrating at the same time the presence of typical species, the absence of dominance of one of these species, and the low abundance of non-typical species, the VCS index fulfils most of the criteria considered as indicators of success by restoration practitioners (Evju et al., 2020).

In many ecosystems we could nonetheless consider that restoration success implies not only the recovery of typical species, but also the spatial organization in a particular assemblage. In coastal sand dunes, the transition between communities (drift line, embryonic, shifting and fixed dunes) is not abrupt (Maun, 2009). Here, we documented that following the restoration, plant communities increasingly become gradually organized along the sea-inland gradient. At the onset of the study, the position on the sea-inland gradient was not a factor explaining the dissimilarity in species composition. However, after 30 years, this had changed dramatically in at least three of the four study sites, indicating that species reorganized according to abiotic filtering. This result was confirmed by the functional analysis. We demonstrated that the functional composition was closer to that in the reference sites after 30 years of restoration than at the beginning of the study for most traits and functional diversity indices. These patterns along the sea-inland gradient, both in reference and restored communities (i.e. decreasing salt affinity,

nutrient affinity, seed mass and increasing SLA, LDMC, functional richness and divergence) are similar to results from previous studies functionally characterizing typical dunes habitats along the Atlantic or Mediterranean shores (Frederiksen et al., 2006; Ciccarelli, 2015; Conti et al., 2017; Torca et al., 2019). Contrary to what was found during the restoration of grasslands in central Europe (Tölgyesi et al., 2019), in our study, the recovery of taxonomic diversity was not slower than the restoration of functional diversity (Appendix S9). This result confirms the high potential of a sand dune community to respond to restoration. The recovery potential could probably be explained by the high level of natural disturbance present in these habitats (e.g. winter storms inducing submersion by seawater and strong erosion; Martínez & Psuty, 2004; Maun, 2009), which induces the presence of a large number of species with high colonization capacities (Maun, 2009; Guja et al., 2010; Yang et al., 2012).

Combined use of β -diversity and functional analyses seems particularly promising as indicators of restoration success. In fact, as in our study system, in many restoration projects we cannot expect a recovery of the full typical species pool for several reasons (e.g. deficit of colonization, priority effect, biogeography). Consequently, instead of evaluating restoration success based solely on the presence/absence of typical species, it may be more efficient to evaluate whether the functional composition is similar to that of reference communities. This strategy offers the possibility to evaluate restoration success on the recovery of similar environmental filtering pressures in restored communities compared with references instead of focusing on the idiosyncrasy of individual taxonomic species recovery (Engst et al., 2016; Carlucci et al., 2020).

4.3 | Strong heterogeneity but similar trajectories among sites

For every metric used (typical species richness, VCS, β -diversity, functional composition and diversity) we found an important site effect, reflecting that despite the use of the same methodology and a relatively similar state before restoration, the results of 30 years of restoration differ among sites. The observation that every restoration is unique is well known by ecological restoration practitioners and scientists, but the reasons behind this are less clear (Stuble et al., 2017). One often-suggested explanation is the priority effect, which proposes that the installation of the first species in a site could prevent the installation of others (Weidlich et al., 2021). However, in our case, this does not seem to be the main reason for the discrepancy among sites, partly because of the plantation of marram grass in every site at the beginning of the restoration. In the two larger sites (Chevret and Verger), we found a globally constant increase in restoration success metrics; however, the situation is much more contrasted in the two other sites (Du Guesclin and Hue). In Du Guesclin site the differences could be attributed to storm perturbations. We found that in 1998 this site was on the same trajectory as the others, but several important storms have since rejuvenated the site, leading to a restart in the succession and consequently

promoting the presence of pioneer species. In the Hue site, the situation seems different with mainly a strong increase in non-typical species, implying modified functional composition. This could be explained by the location of the Hue site in a dense urban matrix, increasing human degradation via species introduction, trampling or other disturbances.

5 | CONCLUSIONS

After 30 years, the restoration of these sand dune plant communities is still not complete and remains heterogeneous among sites, but the results are promising. We demonstrated that restoration operations such as marram grass planting and trampling protection are efficient at promoting an overall recovery in sand accumulation, typical species, sea-inland plant community structuration and community functional traits composition. In the context of severe coastal ecosystem threats, sand dune restoration appears a priority for biodiversity conservation, as well as storm flood protection, but practitioners need to keep in mind that although globally positive, restoration efforts will conduce to different results in each site. In addition, we demonstrate that combined use of taxonomic (VCS index, gamma and beta diversity) and functional approaches is efficient in evaluating restoration success. In particular, functional composition and diversity could be used advantageously to evaluate restoration success because they provide a target that is less susceptible to random processes of species sorting.

AUTHOR CONTRIBUTIONS

All authors contributed to the ideas, design and field sampling of the study; S.C. conducted analyses and led the writing of the manuscript. V.J. and F.R. contributed to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from: <https://doi.org/10.5281/zenodo.7643428>

ORCID

Simon Chollet  <https://orcid.org/0000-0001-5346-5432>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Location map.

Appendix S2. Study sites sand dunes characteristics.

Appendix S3. Number of quadrats sampled per year per sites.

Appendix S4. References community selection.

Appendix S5. Sand accumulation during the first and the last decade of the study.

Appendix S6. Analysis of individual species changes through time.

Appendix S7. Typical and Non-typical species richness per year and site.

Appendix S8. Beta diversity model analysis.

Appendix S9. Functional traits and diversity model analysis.

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