DuneFront

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DuneFront

Realised and potential ecological connectivity of the Demonstrators

DuneFront – D5.3

Deliverable information

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Cover page

Across many European coastlines, traditional grey infrastructure such as dikes provides flood protection but can restrict ecological processes and fragment dune habitats. Dune-in-front-of-dike systems offer a hybrid alternative: they combine engineered coastal defence with natural dune development, buffering waves and storm surges while creating habitat for dune-associated species.

This study evaluates the contribution of these hybrid systems to ecological connectivity, defined here as the ability of species to move between suitable habitat areas. Connectivity is essential for dispersal, recolonization, gene flow and long-term population persistence. When habitats are poorly connected, populations become isolated and more vulnerable to local extinction and environmental change.

We assessed connectivity using a spatially explicit modelling approach that simulates movement, reproduction and settlement across coastal landscapes. Rather than assuming that nearby habitats are connected, the model identifies realised functional connections: links that arise when species successfully disperse and establish in suitable habitat.

For each coastal site, we compared three scenarios:

1. a no-demonstrator scenario without dune-front development;

2. a baseline scenario representing the existing dune-in-front-of-dike intervention; and

3. an extended scenario with additional dune restoration or expansion.

The results show that dune-front development can enhance ecological connectivity, especially when newly created dunes function as stepping stones between existing habitat patches. However, the strength of this effect depends strongly on spatial placement. Creating more habitat is not sufficient on its own; new dunes need to be located where they bridge gaps in the wider coastal network. In some sites, existing interventions already provide substantial connectivity benefits, while further extensions mainly reinforce or expand these networks.

Overall, this study shows that dune–dike hybrid infrastructure can help integrate biodiversity objectives into coastal defence. By accounting for species movement and population persistence, the approach supports planning decisions that better align climate adaptation, coastal safety and biodiversity restoration.

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List of recurring abbreviations

Abbreviation	Explanation
NbS	Nature-based Solutions
DD-hybrid	Dune-dike hybrid
NRR	Nature Restoration Regulation
N2K	Natura 2000
IIC	Integral Index of Connectivity
IBM	Individual-Based Model
LC	Local Connectivity
RC	Regional Connectivity
NS	Node Strength
GIS	Geographic Information System

1. Introduction

1.1 Ecological connectivity as a restoration target in coastal dune landscapes – General objectives

Coastal dunes are dynamic socio-ecological systems that support coastal protection, biodiversity conservation, recreation and landscape identity (Barbier et al., 2011). Within DuneFront, dune–dike hybrid Nature-based Solutions are evaluated as multifunctional interventions that can strengthen coastal safety while restoring or creating dune habitats and associated biodiversity. Work Package 5 assesses the biodiversity performance of these demonstrators across habitats, species, traits and connectivity. Deliverable D5.1 (Mordacq & Dahirel, 2025) quantified the development of Annex I dune habitats in the demonstrator sites, including embryonic dunes, white or blond dunes and later-successional grey dunes. Deliverable D5.2 will assess biodiversity patterns in the demonstrators relative to more natural reference sites, including indications of cross-shore connectivity.

This assessment is framed by European policy on biodiversity conservation, ecological restoration and climate adaptation. The EU Habitats Directive aims to maintain or restore natural habitats and species of Community interest at favourable conservation status and provides the basis for the Natura 2000 network (Council Directive 92/43/EEC). Together with the Birds Directive, which requires Member States to preserve, maintain or re-establish sufficient diversity and area of habitats for wild birds, these directives form the core legal framework for Natura 2000 and are directly relevant to coastal dune systems as habitat complexes for specialised plant, invertebrate and bird communities (Directive 2009/147/EC).

More recent European policy further emphasises ecological networks and restoration at larger spatial scales. The EU Biodiversity Strategy for 2030 frames biodiversity recovery as a central element of the European Green Deal and calls for a coherent Trans-European Nature Network, including ecological corridors and better-connected protected areas (European Commission, 2020). This direction is reinforced by the EU Green Infrastructure strategy, which promotes strategically planned networks of natural and semi-natural areas that deliver ecosystem services while enhancing biodiversity and connectivity (European Commission, Green Infrastructure). The Nature Restoration Regulation further strengthens this framework by setting binding restoration objectives for degraded ecosystems across the EU, including restoration measures covering at least 20% of EU land and sea areas by 2030 and all ecosystems in need of restoration by 2050 (Regulation (EU) 2024/1991). For DuneFront, this policy context is directly relevant because the Regulation builds on existing EU nature legislation, includes habitats such as dunes, and emphasises the need to improve and re-establish biodiverse habitats at large spatial scales (Regulation (EU) 2024/1991; European Commission, 2020).

D5.3 extends the habitat- and species-based assessments by evaluating the regional ecological connectivity of the DuneFront demonstrators. Habitat area alone does not determine ecological performance: habitat patches must also be functionally connected to support dispersal, recolonization, demographic rescue, gene flow and long-term metacommunity persistence. Habitat loss and fragmentation are major drivers of biodiversity decline because they reduce movement opportunities and weaken ecological processes that maintain viable populations, including rescue effects and genetic exchange (Brown & Kodric-Brown, 1977; Templeton et al., 1990; Lande et al., 1998; Haddad et al., 2015; IPBES, 2019; Newbold et al., 2015).

Connectivity is especially important in coastal dune landscapes, where suitable habitats are often embedded in fragmented and urbanised coastal zones. Hard coastal infrastructure, roads, promenades, ports, recreational infrastructure and stabilisation measures can interrupt habitat continuity and limit movement along the coast. Coastal dunes also function as meta-ecosystems, where biodiversity and resilience depend on flows of organisms, sediment, energy and materials across spatial scales. From this perspective, DuneFront demonstrators should be evaluated not only as local habitat-creation measures, but also as potential stepping stones or connectivity nodes within wider coastal ecological networks.

1.2 Cross-shore and alongshore connectivity in dune systems

Connectivity in coastal dunes operates along two complementary spatial dimensions. Cross-shore connectivity refers to exchanges of sand, salt spray, carbonate, organic material and organisms between the beach, foredune and inland dune zones. These flows maintain the geomorphological and biogeochemical processes that structure dune vegetation, support early-successional habitats and contribute to dune growth and storm-buffering capacity (McLachlan et al., 2025). Alongshore connectivity refers to the movement of organisms between dune patches along the coastline. It supports dispersal, gene flow, recolonization after disturbance, metapopulation viability and range shifts under climate change.

D5.3 focuses primarily on regional alongshore ecological connectivity. While D5.1 assessed whether demonstrators create or maintain suitable dune habitat locally, D5.3 evaluates whether these habitats are integrated into the wider coastal network. This distinction is central to the ecological assessment of Nature-based Solutions. A demonstrator may create valuable local habitat, but its long-term biodiversity contribution may remain limited if that habitat is isolated. Conversely, a small intervention can have high ecological value when it bridges a gap between existing dune patches (e.g. Hanski 1999).

1.3 Why single-species connectivity models are insufficient

Ecological connectivity is species-dependent. Species differ in dispersal distance, habitat specificity, fecundity, thermal tolerance, demographic sensitivity, and persistence in small or isolated patches. A landscape that is connected for a highly mobile generalist may therefore remain fragmented for a less mobile or more specialized species. Connectivity assessments based on a single focal or surrogate species can consequently misrepresent the needs of the wider ecological community (Meurant et al., 2018; Wood et al., 2022).

This limitation is increasingly recognised in multispecies connectivity research. Wood et al. (2022) define multispecies connectivity analysis as the identification of habitat networks and movement pathways that support the long-term persistence of multiple species. They show that single-species surrogates often poorly represent community-wide connectivity needs, whereas generic or virtual species can provide a useful compromise when empirical data or computational capacity are limited.

This issue is particularly relevant for dune restoration. Coastal dune biodiversity consists of communities of plants, arthropods and other organisms with contrasting ecological strategies. Some species may rapidly colonise newly created dune habitats, whereas others are dispersal-limited or depend on specific successional stages. Evaluating demonstrator performance therefore requires a community-level perspective on connectivity, rather than reliance on a single target species.

1.4 Arthropods, virtual species and trait-based representation of communities

A central challenge in community-level connectivity modelling is the lack of detailed empirical data for most species. This is especially relevant in dune ecosystems, where many ecologically important organisms remain poorly documented in terms of dispersal, demography and habitat use. Arthropods are a key group in this context. They contribute to pollination, decomposition, nutrient cycling and trophic interactions, but remain less represented in conservation research and monitoring than vertebrates (Cardoso et al., 2011; Wagner et al., 2021; Logghe et al., 2025a).

Arthropods are well suited for assessing ecological connectivity in coastal dune landscapes. Many are mobile enough for landscape structure and habitat continuity to influence dispersal and colonisation, but generally not so mobile that regional habitat discontinuities become irrelevant, as may be the case for many vertebrates. Unlike many plants, they can move independently, without relying primarily on wind, water or animal-mediated seed dispersal. Arthropods therefore represent an informative intermediate group for testing whether dune-front interventions function as stepping stones or connectivity nodes in fragmented coastal landscapes.

Arthropods also vary strongly in movement capacity and dispersal mode. Cursorial species may be constrained by local habitat discontinuities, whereas flying species can disperse over longer distances. Even in flying species, however, realised dispersal is limited by life-history traits, body size, reproductive strategy, thermal niche and habitat specialisation (Bonte et al., 2012; Logghe et al., 2025b). This trait variation makes arthropods particularly useful for community-level connectivity modelling, because restoration may improve connectivity for some functional groups while leaving others constrained by the spatial configuration of suitable habitat.

The focus on arthropods is further justified by recent evidence of insect and arthropod declines. Long-term monitoring in German protected areas documented a decline of approximately 76% in seasonal flying insect biomass over 27 years, with a mid-summer decline of 82% (Hallmann et al., 2017). A global review identified habitat loss, conversion to intensive agriculture and urbanisation, pollution, biological invasions and climate change as major drivers of insect decline (Sánchez-Bayo & Wyckhuys, 2019). These declines have been described as a “death by a thousand cuts”, reflecting the cumulative impact of interacting pressures such as land-use intensification, habitat loss, pollution, climate change and invasive species (Wagner et al., 2021).

Virtual species provide a practical way to address incomplete species-level information. Rather than representing named species, they describe ecologically plausible combinations of traits associated with groups of organisms that share similar ecological characteristics. This approach allows multiple ecological strategies to be included without requiring complete empirical data for every species. When trait combinations are derived from empirical trait distributions, simulated species remain biologically plausible while still representing broader community-level responses (Santini et al., 2016; Mimet et al., 2016; Sahraoui et al., 2017; Wood et al., 2022; Prima et al., 2024).

This trait-based approach is increasingly feasible for arthropods. Recent work compiled life-history, dispersal, thermal-niche and ecological traits for 4,874 northwestern European arthropod species across ten orders, including body size, fecundity, development time, voltinism, lifespan, dispersal capacity, thermal niche, feeding guild and habitat preferences (Logghe et al., 2025a). Further analysis of this database showed consistent covariation among dispersal, life-history and thermal-niche traits across arthropod orders. Species with faster life-history strategies tended to have higher dispersal capacities and broader thermal niches than slower species (Logghe et al., 2025b). These datasets provide an empirical basis for generating virtual arthropod species with realistic trait combinations rather than arbitrary parameter sets.

D5.3 therefore uses arthropod-inspired virtual species to represent a range of dispersal capacities and life-history strategies. By simulating multiple virtual species, the model accounts for the fact that connectivity restoration may benefit different components of the community in different ways. Highly mobile flying species may respond to broad-scale habitat continuity, whereas less mobile or cursorial species may depend more strongly on local habitat continuity and stepping-stone structure. This makes the assessment more robust than a single-species or single-surrogate approach and better aligned with the DuneFront objective of evaluating demonstrator performance across habitats, species, traits and ecological connectivity.

1.5 Scenario-based evaluation of demonstrator performance

D5.3 evaluates whether the DuneFront demonstrators (Figure 1.1) improve regional ecological connectivity and whether further dune-front restoration could generate additional gains. Each site is assessed under three spatial scenarios. The baseline scenario represents the current demonstrator configuration. The no-demonstrator scenario represents the counterfactual situation without the existing NbS intervention. The extended restoration scenario represents a potential future configuration with additional dune habitat in front of urban infrastructure.

Two scenario contrasts are used to evaluate performance. The baseline versus no-demonstrator comparison estimates the realised contribution of the existing demonstrator. The extended versus baseline comparison estimates the additional connectivity gain that could result from scaling up dune-front restoration. This approach links demonstrator performance to broader connectivity-based restoration thinking, where interventions are evaluated not only as local habitat measures but also by their effect on ecological networks, cross-scale flows and long-term resilience.

The analysis addresses three questions:

1. Do existing demonstrators improve regional ecological connectivity relative to a no-demonstrator situation?
2. Which sites show the strongest realised connectivity benefit?
3. Where would extended dune-front restoration generate the greatest additional connectivity gains?

Figure 1.1. Location of the 13 European sites used in WP5.3 *(the 12 demonstrators in the DuneFront project with Belgian ones merged) (image from https://dunefront.eu/, modified by the authors).*

2. Methodology

2.1 Study domain and demonstrator sites

2.1.1 Demonstrator selection

Regional connectivity analyses were conducted for all DuneFront demonstrator sites (Figure 1.1). The DuneFront demonstrators include urbanised and semi-urbanised dune-front systems in Belgium, the Netherlands, France, Germany, Portugal and Sweden. The three Belgian sites were analysed as a single regional case (hereafter, BE_combined). This was done because the Belgian coast is highly urbanised and the individual demonstrator locations are close to each other and embedded within a broader, spatially connected coastal context. Treating them as one regional case allowed their collective contribution to alongshore connectivity to be assessed, rather than evaluating each intervention as an isolated local element. The analysed sites were thus: BE_combined, DE_StPeterOrding, FR_Dunkerque, FR_Soulac, FR_SteMarie, NL_HondsbosscheDuinen, NL_Katwijk, NL_Sandmotor, NL_Texel, PT_Porto and SE_Ystad.

The selected demonstrators should therefore not be interpreted as a statistically random sample of European dune systems. Instead, the analysis provides a scenario-based assessment of the DuneFront demonstrator portfolio. Its purpose is to compare how different demonstrator configurations contribute to regional ecological connectivity and to identify where additional dune-front restoration could most effectively strengthen functional habitat networks. This complements D5.1, which focused on habitat and vegetation development within the demonstrators, by assessing whether these habitats are functionally connected within the wider coastal landscape.

2.1.2 Spatial extent of regional connectivity analyses

For each demonstrator, regional connectivity was analysed within a landscape window centred on the demonstrator location. The simulation domain consisted of the land area in a circular area with a 10 km radius around the demonstrator centre point (merged in the case of BE_combined). Habitat and carrying capacity were represented on a 100 × 100 m grid, and grid cells were used as potential habitat nodes in the connectivity model.

Carrying capacity (*K*) was calculated for each 100 × 100 m grid cell as a value proportional to the area of suitable dune habitat contained within that cell after rasterization of the habitat polygons. Cells with no suitable habitat received $K = 0$, while cells with greater habitat coverage received higher carrying-capacity values. To maintain computational efficiency, K was scaled to a maximum value of 10 (see section simulations). Thus, carrying capacity should be interpreted as a relative measure of habitat availability rather than an empirically derived estimate of population size

The same spatial domain was used for the no-demonstrator, baseline demonstrator and extended restoration scenarios within each site. This ensured that differences among scenarios reflected changes in habitat availability, carrying capacity and realised dispersal links, rather than differences in the geographic extent of the analysis. Maintaining a constant spatial context within each demonstrator was therefore essential for comparing scenario-specific connectivity metrics.

Each exported node represented a raster cell included in the simulated network and was associated with spatial coordinates, carrying capacity and local network properties. The local node files contained co_x and co_y coordinates, carrying_capacity, and the graph-based node strength metric. Cells with positive carrying capacity represented habitat cells available to the ecological simulation, whereas cells with non-zero node strength represented locations that participated in realised dispersal connections.

For mapping and interpretation, the full node set was retained to preserve the spatial context of each simulated network. Habitat cells and connected subsets were then used to identify where functional connectivity was concentrated within the landscape. Local connectivity maps, such as those based on node strength, were produced from the exported node coordinates. To avoid confounding scenario differences with changes in map extent, maps and local network summaries were interpreted using the union of nodes represented across the three scenarios wherever possible.

The regional analyses should therefore be understood as site-specific landscape assessments around each demonstrator. Although the modelling domain was defined consistently around each demonstrator centre, the resulting networks differed among sites because coastal configuration, urbanisation, surrounding dune habitat and scenario-specific habitat availability varied strongly. This approach allowed each analysis to capture the neighbouring habitat elements most relevant for alongshore connectivity, stepping-stone function and regional metacommunity dynamics.

2.2 Spatial input data and habitat representation

For the boundaries of each demonstrator site, we used shapefiles that were previously made available within the DuneFront project (Robin et al., 2024). Information about the location of existing dunes (excluding demonstrators) was primarily sourced from the EU's Coastal Zones layer (Copernicus Land Monitoring Service, 2021), which we clipped to the simulation extents described in Section 2.1.2. This vector spatial layer maps all coastal regions of Europe (to an inland depth of 10 km) and classifies them in habitats polygons at fine resolution (minimum mapping unit 0.5 ha, minimum mapping width 10 m). However, while this layer contains a "dunes" class (code 62120), cross-examination against aerial imagery showed that simply using that class as our reference habitat would not be suitable. Indeed, given that coastal habitats are often small, many actual dunes were frequently lumped with or misclassified as beaches, intertidal flats, grassland, shrubland or similar habitats. Therefore, we first filtered the layer to only keep land use/land cover classes that could include open dunes (14000 Green urban, sports and leisure facilities, 42100 Semi-natural grassland, 51000 Heathland and moorland, 61100 Sparse vegetation on sands, 62111 Sandy beaches, 62120 Dunes, and (more rarely) 53000 Sclerophyllous scrubs, 61200 Sparse vegetation on rocks, 72100 Salt marshes, 72300 Intertidal flats). We then examined every remaining polygon in our simulation extents and decided to keep or remove it based on checking OpenStreetMap and Google Maps/Google Street View imagery. In cases where dune habitat was included within a much larger non-dune polygon (e.g. dunes mapped as part of a beach polygon, or fixed dunes merged with adjacent lawn areas), we manually extracted the dune area from the larger patch. This step was necessary because retaining the entire patch would overestimate dune habitat, whereas removing it altogether would underestimate dune density. In a small number of cases, we also manually digitized additional dune polygons from satellite imagery when dunes had been assigned to land-cover classes not included in our initial selection.

To identify areas with restoration potential, we delineated 50 m-wide linear buffers along the beach side of all beach–inland boundaries that were not already adjacent to a dune polygon or a demonstrator site. These buffers represent potential habitat that could be restored under the extended scenario. The selected width approximates the typical cross-shore extent of the dune–dike hybrid demonstrators considered in this study. The location of the existing dunes areas and potential beaches for the extended design are visualised in Figure 2.2.

2.3 Scenario design

The connectivity analysis was based on comparing three spatial scenarios: a baseline scenario, a no-demonstrator scenario, and an extended restoration scenario (Figures 2.2, 2.3). Together, these were used to separate the realised connectivity contribution of existing DuneFront interventions from the additional gain that could potentially be achieved through further dune-front restoration. For each scenario, we rasterized the polygon layers described in 2.2 above in R, using the sf and terra packages (100m grid resolution, R Core Team 2025; Pebesma; 2018, Hijmans, 2026). Briefly: grid cells overlapping with any of the polygons were considered as potential or actual habitats and to be included as network nodes; other grid cells were set to NA. The carrying capacity of each grid cell was set to a value proportional to the area covered by the polygons considered as habitats under the scenario considered.

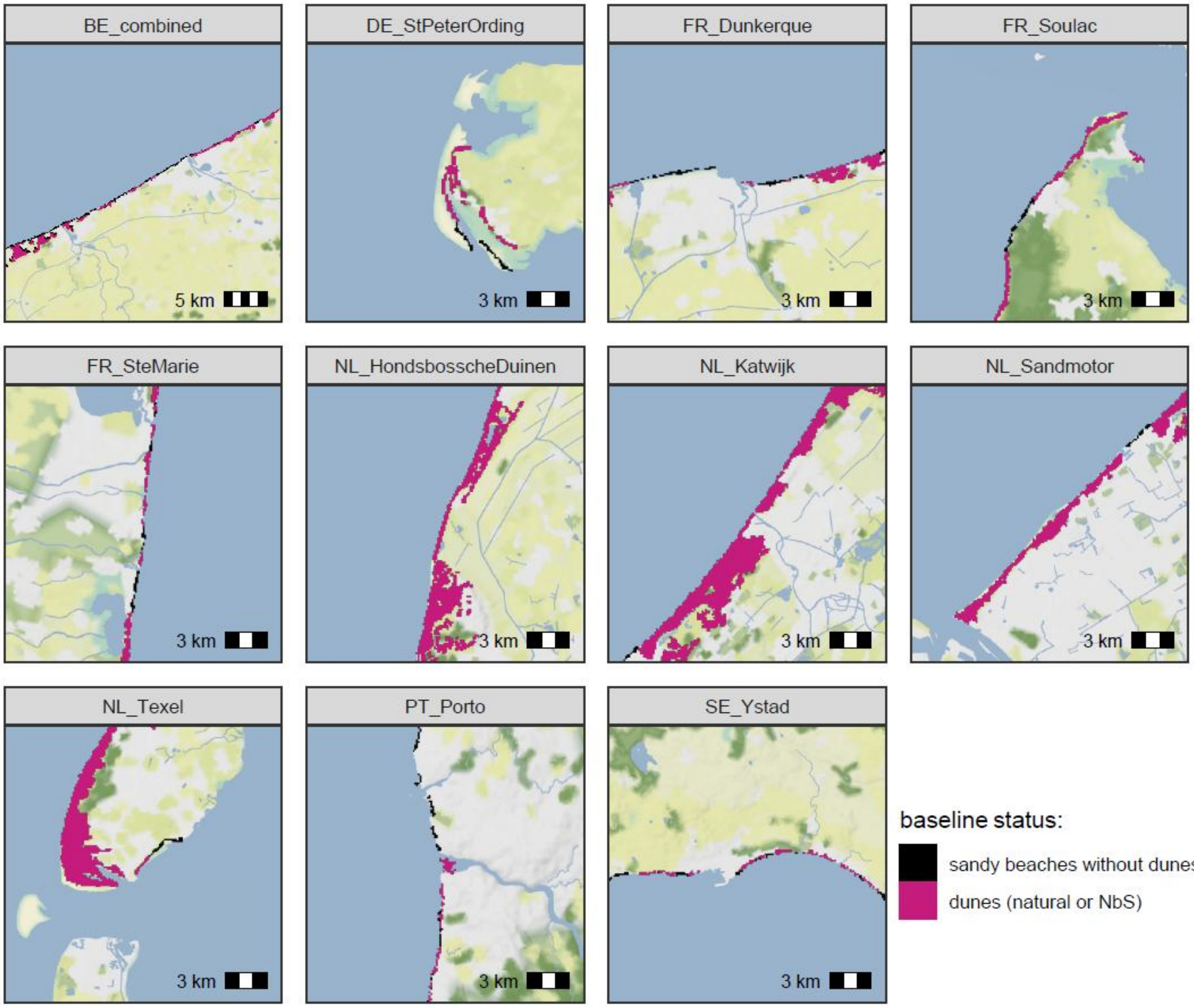


Figure 2.2. *Baseline distribution of sandy coastal habitat across the ten DuneFront demonstrator landscapes. Black areas indicate sandy beaches without dunes, while magenta areas represent existing dunes, including both natural dunes and previously established nature-based solutions (NbS). The maps provide the spatial context of the demonstrators used in subsequent scenario analyses and identify locations where future dune expansion scenarios were evaluated. For NL_Texel, only sandy coasts on Texel Island itself are included. Note the difference in scale between BE_combined and the other landscapes. Map backgrounds are © Stadia Maps © Stamen Design © OpenMapTiles © OpenStreetMap contributors.*

2.3.1 Baseline scenario

The baseline scenario represents the current demonstrator configuration. It includes as habitats both the polygons associated with the existing demonstrator intervention, and the surrounding existing dune regional habitat network. This scenario was used as the reference state for assessing present-day demonstrator performance and as the starting point for evaluating additional restoration potential.

2.3.2 No-demonstrator scenario

The no-demonstrator scenario represents a counterfactual configuration in which the existing demonstrator is absent. In practical terms, the habitat contribution associated with the demonstrator was removed, while the surrounding regional habitat network was retained.

This scenario was compared with the baseline to estimate the realised contribution of the current intervention to regional ecological connectivity. Because the broader landscape context was kept unchanged, differences between the two scenarios can be attributed to the presence or absence of the demonstrator-associated habitat within the modelled network.

2.3.3 Extended restoration scenario

The extended restoration scenario represents a potential future configuration in which additional dune habitat is created or restored beyond the current demonstrator footprint, typically in front of urban or hard coastal infrastructure. In practice, all polygons described in 2.2, including the beach-side linear buffers, were here considered as habitats when rasterizing. This scenario was compared with the baseline scenario to evaluate whether scaling up dune-front restoration could further strengthen regional ecological connectivity. Differences between these scenarios therefore represent the additional connectivity effect of the proposed restoration extension, conditional on the assumptions used to define suitable habitat and carrying capacity. Due to the already continuous dune coverage along the NL_HondsbosscheDuinen coastline, no extended scenario was generated for this site.

2.3.4 Assumptions and limitations of scenario construction

The scenario design provides a structured basis for comparing demonstrator effects, but several assumptions need to be considered when interpreting the results.

First, the scenarios are simplified representations of current, counterfactual and potential future habitat configurations. The no-demonstrator scenario assumes that the demonstrator-associated habitat can be removed while keeping the surrounding landscape unchanged. This provides a useful estimate of the demonstrator's contribution, but it does not reconstruct the full historical trajectory that might have occurred in the absence of the intervention.

Second, the extended restoration scenario should be interpreted as a potential restoration configuration rather than as a predicted future state. It assumes that additional dune habitat can be created or restored in the selected locations and that this habitat can function as suitable habitat within the modelled network (see figure 2.2, cells in black). The resulting connectivity gain is therefore a modelled potential, not a guaranteed ecological outcome.

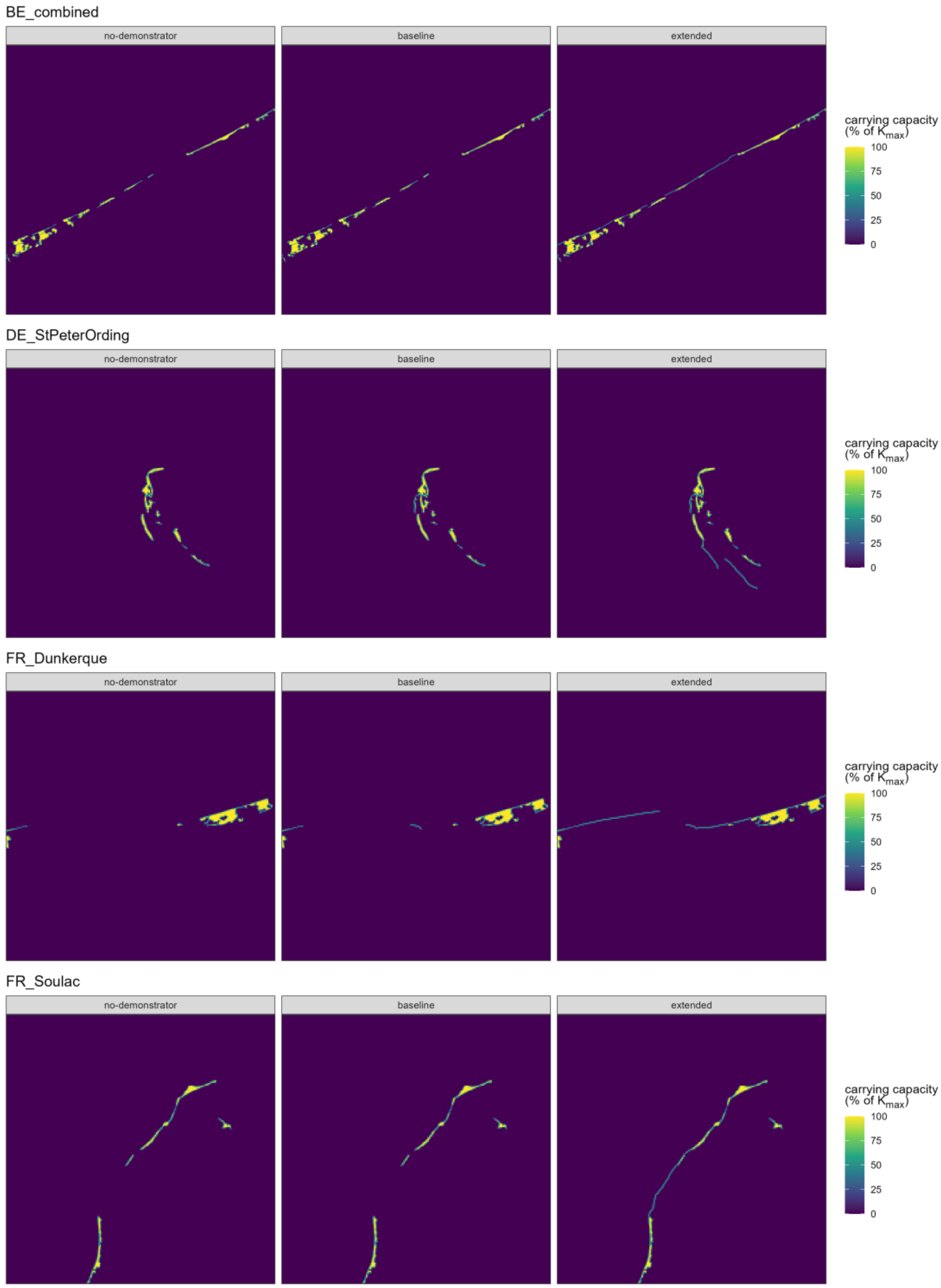
Third, all scenarios rely on the habitat and carrying-capacity representation used in the simulations. Habitat cells included in the model are treated as suitable for the arthropod-inspired virtual species, but real habitat quality may vary among sites and through time. Newly created or restored dunes may differ in vegetation structure, successional stage, sand dynamics, disturbance regime, microclimate and resource availability (see D5.1, and upcoming D5.2). The results should therefore be interpreted as estimates of potential functional connectivity, conditional on the development of suitable dune habitat.

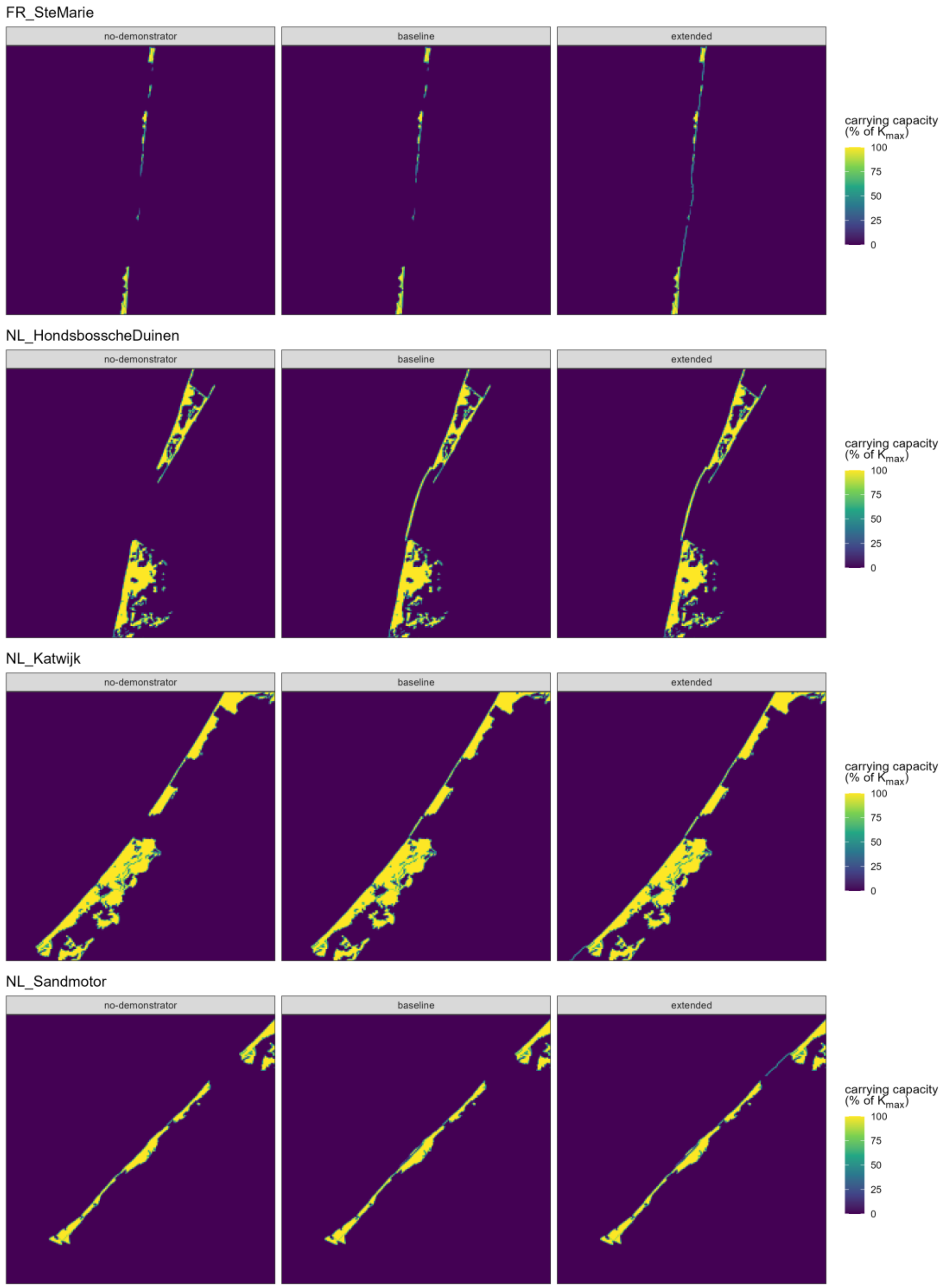
Fourth, connectivity metrics depend on the spatial domain and node set used to construct the network. Scenario comparisons were therefore interpreted within their own comparison context: the local demonstrator effect was assessed from the baseline versus no-demonstrator contrast, whereas extended-restoration effects were assessed from the extended versus baseline contrast. This avoids comparing values across contexts where the underlying scenario representation may differ.

Fifth, only grid cells that overlap with one of the actual or potential dune polygons are included as node networks. This implies that the virtual species simulated are all specialist species that can only use open dune and beach habitats. While dunes also harbour generalist arthropod species (Van De Walle et al. 2025), this is a necessary simplification, and these dune specialists are besides target species for conservation also the ones most likely to benefit from dune restoration actions.

Finally, the analysis evaluates simulated functional connectivity for arthropod-inspired virtual species. It does not directly verify whether all modelled dispersal pathways are used by real species in the field. The results should therefore be interpreted together with habitat-development information from D5.1, biodiversity monitoring and future empirical observations of colonisation and community development.

2.3.5 Overview of the scenarios for each location




FR_SteMarie
no-demonstrator
baseline
extended
carrying capacity (% of K_{max})
100
75
50
25
0
NL_HondsbosscheDuinen
no-demonstrator
baseline
extended
carrying capacity (% of K_{max})
100
75
50
25
0
NL_Katwijk
no-demonstrator
baseline
extended
carrying capacity (% of K_{max})
100
75
50
25
0
NL_Sandmotor
no-demonstrator
baseline
extended
carrying capacity (% of K_{max})
100
75
50
25
0

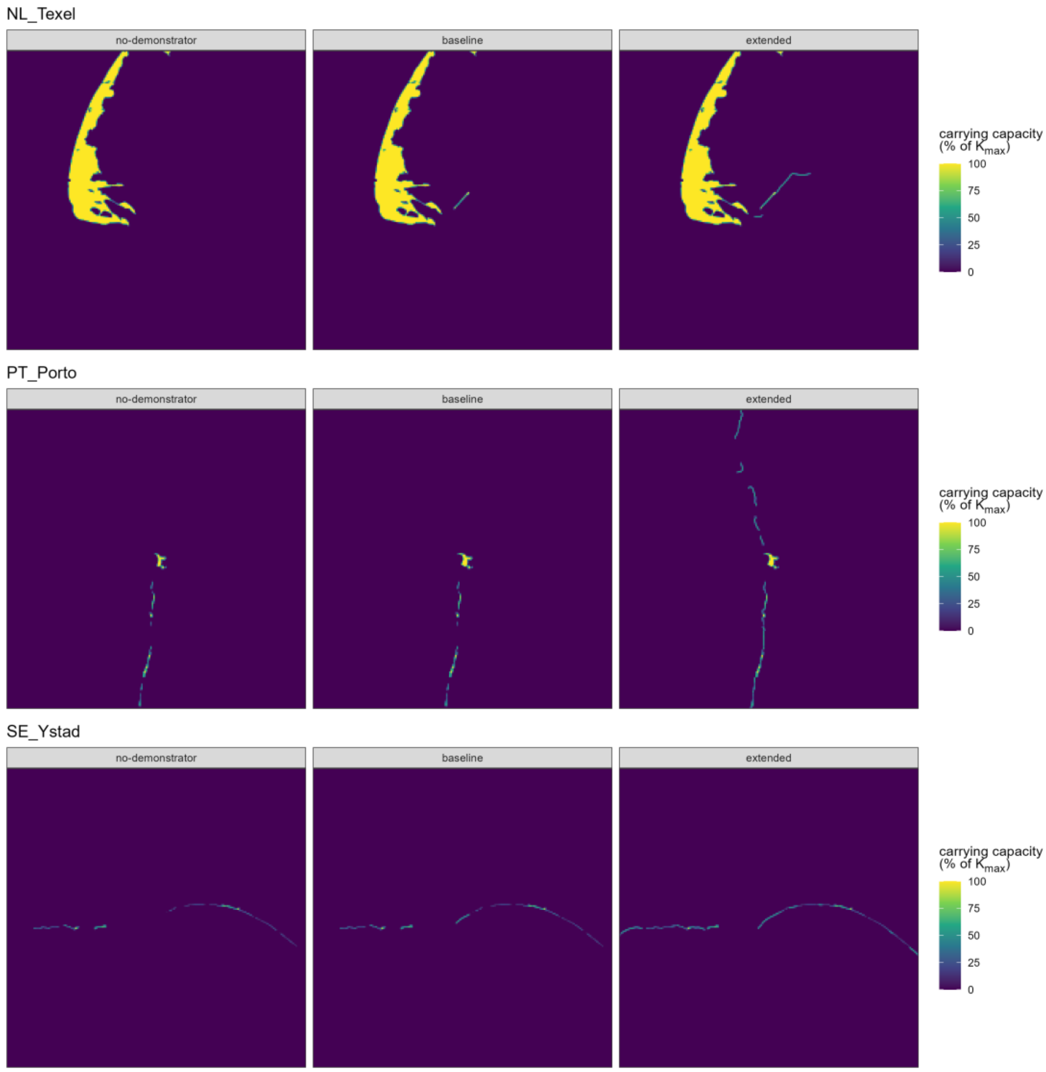


Figure 2.3. Overview of the modelled connectivity scenarios for all included demonstrators. *The baseline scenario (mid panels) is the current situation with the demonstrator in place. The 'no demonstrator scenario' simulates the situation if the demonstrator had not been installed, the extended scenario the potential for a maximal connectivity restoration through dune-dike hybrids in the selected location.*

2.4 Community-modelling framework

2.4.1 Model overview and process flow

Regional ecological connectivity was simulated with a modular, spatially explicit metacommunity modelling framework. The model consists of three main components: a

Landscape module, a Metapopulation module and a set of Demography modules. The Landscape module stores the spatial habitat configuration and cell-level carrying-capacity values. The Metapopulation module manages the distribution and abundance of virtual species across the landscape. The Demography modules simulate local population dynamics, emigration, dispersal and settlement.

Each study area was represented as a gridded regional landscape with scenario-specific habitat status and carrying capacity. The same modelling framework was applied to the no-demonstrator, baseline demonstrator and extended restoration scenarios. Differences among scenarios therefore arose from changes in habitat configuration and carrying capacity, while the demographic and dispersal rules remained constant.

The model simulates arthropod-inspired virtual species rather than named species. The community consist of 20 virtual arthropods. Each virtual species is defined by a small set of life-history and movement-related traits: body size, dispersal capacity, temperature optimum, temperature range, and fecundity. These traits determine how species differ in population build-up, reproductive output and movement among habitat cells.

Within each scenario, populations are initialised in suitable habitat cells and then simulated through repeated generation-based life cycles. A total of 50 generations are modeled per simulation. Each generation includes local demographic growth, density-dependent emigration, stochastic dispersal and post-dispersal settlement. Cells with zero carrying capacity are treated as unsuitable habitat and cannot support settled populations.

The main output used for the connectivity analysis is the set of successful dispersal and settlement events generated during the simulations. These realised movements form the basis for the connectivity networks described in Section 2.5. In this framework, functional connectivity is not inferred directly from geographic proximity or habitat adjacency. It emerges from the interaction between habitat configuration, carrying capacity, virtual-species traits, demographic dynamics and successful settlement.

The general workflow can be summarised as follows (see figure 2.4.1):

1. scenario-specific habitat and carrying-capacity layers are loaded into the Landscape module;
2. virtual species are created by combining traits in a realistic way using the life history covariation patterns as derived from the trait database;
3. virtual-species populations are initialised in suitable habitat cells;
4. local demographic growth and reproduction are simulated;

5. density-dependent emigration determines which individuals disperse;
6. dispersal distance and direction are drawn stochastically;
7. individuals arriving in suitable cells may settle, subject to carrying capacity;
8. density dependent population regulation controls the demographic growth;
9. successful source–destination movements are recorded for network construction.

The model is implemented in Python and is intended for public release once the broader modelling framework has been finalised.

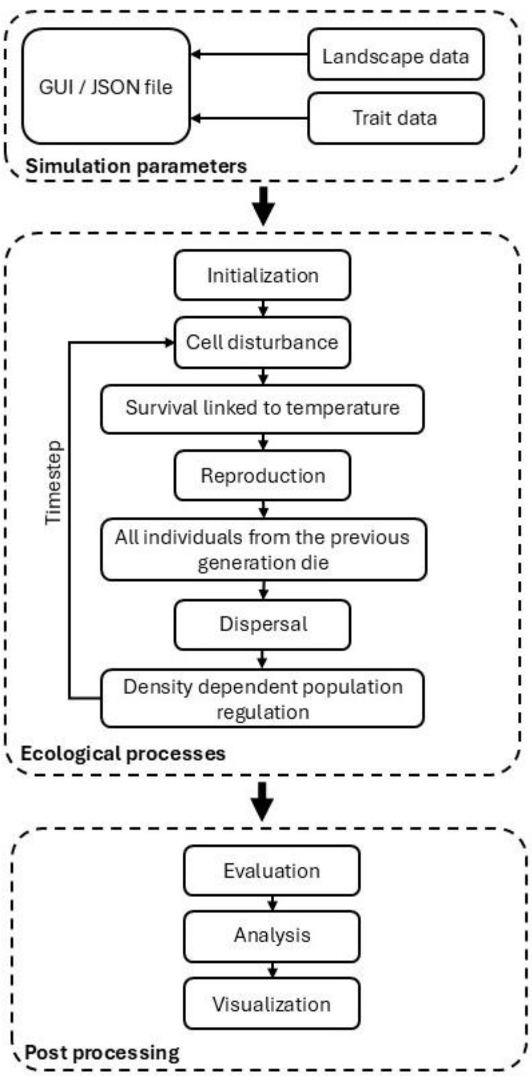


Figure 2.4.1 General workflow of the ecological connectivity modelling framework. *Landscape data and species-trait data are combined with user-defined simulation parameters to initialise a spatially explicit metacommunity model. During each timestep, populations are subjected to disturbance, temperature-dependent survival, reproduction, dispersal and density-dependent population regulation. The resulting dispersal networks are subsequently evaluated using graph-based connectivity metrics and summarised through statistical analyses and visualisation outputs.*

2.4.2 Virtual species and trait-based parameterisation

The simulations used a trait-based virtual-species approach to represent a range of arthropod ecological strategies relevant to dune connectivity. Virtual species were parameterised using empirical distributions (and covariations) of arthropod trait values in Logghe et al. (2025a,b), following earlier virtual-species modelling work in which body size was used as a central trait for deriving biologically plausible combinations of life-history and dispersal characteristics (Figure 2.4.2).

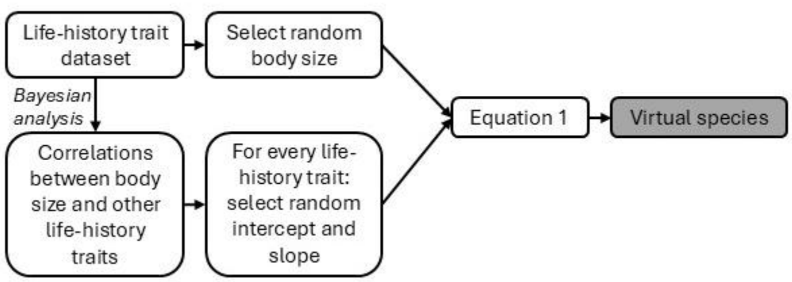


Figure 2.4.2. Construction of virtual species from empirical arthropod trait distributions. *Virtual species are generated using trait correlations derived from a Bayesian analysis of the life-history trait database. Body size is first sampled from the empirical distribution and subsequently used to derive correlated values for dispersal and fecundity. Random variation in regression parameters allows the generation of multiple ecologically realistic trait combinations representing different arthropod strategies.*

A total of 20 virtual species were created to simulate the metacommunity. Each virtual species was characterised by five traits: body size, dispersal capacity, temperature optimum, temperature range, and fecundity. Coleoptera are here used as the model system given their representative life history for other insect orders (Logghe et al. 2025b). Body size was retained as a central trait axis because it covaries with several ecological and life-history characteristics. Dispersal capacity determines potential movement among habitat cells, whereas the thermal traits and fecundity influence local population build-up after establishment. Together, these traits determine whether a virtual species can colonise suitable dune habitat, persist locally and contribute to realised dispersal links.

The same virtual-species pool and parameterisation were used across all scenarios. Scenario comparisons therefore reflect changes in habitat configuration and carrying capacity rather than changes in the simulated species community. This makes it possible to assess how the same trait-based arthropod community responds to the presence, removal or expansion of dune-front habitat.

Carrying capacity (*K*) was assigned at the grid-cell level and varied among scenarios according to habitat availability (Section 2.1.2). It should be interpreted as a pseudo-carrying capacity that regulates local population size, density-dependent emigration and post-dispersal settlement rather than as an empirically derived demographic parameter. The same cell-specific *K* was applied to all virtual species, without accounting for differences in body size, resource use or interspecific competition. To maintain computational efficiency, *K* values were scaled to a maximum of 10 while preserving relative differences among cells and scenarios. Cells with higher *K* supported larger populations and generated more dispersers, thereby contributing more strongly to the realised connectivity network.

The resulting networks should be interpreted as potential functional connectivity networks for a trait-based arthropod community. The parameterisation captures variation in movement capacity and population build-up, but does not represent named species or the full range of processes affecting dune arthropods. Habitat specialisation, trophic interactions, phenology, genetics and fine-scale microhabitat quality were not explicitly included.

2.4.3 Demography, dispersal and settlement

After initialisation, each virtual species was simulated through repeated generation-based life cycles. Each generation consisted of three linked stages: local demographic update, emigration and dispersal, and post-dispersal settlement.

Local demographic dynamics were governed by species-specific survival linked to their temperature traits and fecundity, together with the carrying capacity of the occupied cell. Population size was regulated by local carrying capacity, so that suitable cells could support persistent populations only up to their assigned capacity. Cells with zero carrying capacity were unsuitable and could not retain individuals. Stochastic decreases in a cell's carrying capacity were simulated to mimic the temporal disturbances that often shape metapopulation dynamics in natural systems.

Emigration was modelled as a density-dependent process. Individuals or offspring were more likely to leave a cell when local density approached or exceeded the cell’s carrying capacity. This links dispersal to local demographic pressure: high-capacity cells can support larger populations and may produce more dispersers, whereas low-capacity cells generate fewer dispersal events. Movement distances were determined by the species-specific dispersal capacity. The dispersal capacity trait is a value between zero and one and represents both the probability of dispersal and the relative distance an individual can travel. This trait is used to scale species relative to one another in terms of dispersal ability, where one represents the most dispersive species and zero the least dispersive. This value is then multiplied by the dispersal multiplier to obtain the species-specific mean travel distance (X_{mean}). The dispersal multiplier represents the average distance the most dispersive virtual beetle will travel (thus the virtual beetles with a dispersal trait equal to one). The simulation used a distance multiplier of 5 km. Using the species-specific X_{mean} a dispersal kernel for each species is created. This kernel follows a fat-tailed Pareto distribution from which the dispersal distances can be drawn, allowing frequent short-distance movements and occasional long-distance dispersal events. These rare longer movements are relevant for assessing stepping-stone function and connectivity among fragmented dune patches. Dispersal is mediated by the following equations:

$$X_{mean} = dispersal\ capacity\ value \times dispersal\ multiplier$$

$$travel\ distance = \frac{\frac{\alpha - 1}{\alpha} \times X_{mean}}{U^{\frac{1}{\alpha}}}$$

The parameter α determines the shape of the distribution tail. To ensure that individuals from the same species do not disperse identical distances, the random value *U* (between 0 and 1) is also included in the Pareto distribution.

Movement direction was random. Individuals did not actively select target cells based on habitat quality. As a result, dispersal success depended on both the species' movement capacity and the spatial configuration of suitable habitat around the source cell. A dispersal event was unsuccessful when an individual moved outside the analysis domain or landed in a cell with zero carrying capacity. Such individuals were removed from the simulation. Individuals arriving in suitable cells entered the settlement stage, where local carrying capacity again constrained persistence. If the number of individuals in a receiving cell exceeded its carrying capacity, surplus individuals were removed through a random competition step, meaning that no priority effects were included. Since carrying capacity is defined at the species-level, species do not interact with each other in this process. Therefore, only intraspecific competition is modelled.

Successful dispersal and settlement events were recorded for subsequent network construction. A recorded movement therefore represents a realised source–destination connection: the source cell produced a disperser, the individual reached a suitable destination cell, and settlement was possible after local density filtering. To allow for a burn-in period, only the movements occurring in the last 10% of the model runtime are included in the final connectivity network. In this simulation, this corresponds to the movements from the last five timesteps.

The demographic and dispersal procedure can be summarised as follows:

For each virtual species and generation:

1. **Local population update**
   - population growth and/or offspring production
   - regulated by species-specific temperature traits and fecundity
2. **Density-dependent emigration**
   - local density evaluated relative to carrying capacity
   - emigration probability increases when local density approaches or exceeds capacity
3. **Stochastic dispersal**
   - dispersal distance determined by dispersal kernel
   - dispersal direction random
   - individuals leaving the domain or landing in unsuitable cells are lost
4. **Settlement and competition**
   - individuals arriving in suitable cells may establish
   - local population size is filtered according to carrying capacity
5. **Connectivity recording**
   - successful source–destination movements in the last 10% of the runtime are stored
   - recorded movements form the basis for the functional connectivity network

This modelling structure means that a restored dune cell contributes to regional connectivity only when it can support individuals and exchange successful dispersers with other suitable cells. Habitat cells that are spatially present but isolated, low in carrying capacity or rarely reached by dispersers contribute less to the realised network.

2.4.4 Simulation outputs used for connectivity-network construction

The connectivity analysis used simulation outputs related to habitat capacity and successful dispersal. For each demonstrator and scenario, two types of output were retained:

- cell-level carrying capacity;
- successful dispersal and settlement events between cells.

Outputs were stored at two complementary levels. First, local node-level outputs were produced for each scenario. These files contained a node identifier, spatial coordinates, carrying capacity and local graph metrics, including degree centrality, betweenness, in-closeness, out-closeness, eigenvector centrality, clustering and node strength (Urban & Keitt, 2001; Minor & Urban, 2008; Galpern et al., 2011). Node strength was used for the demonstrator-level maps because it summarises the total intensity of realised connections associated with each habitat node.

Second, regional network-level outputs were produced for each demonstrator and scenario. These outputs summarised the overall structure of the scenario-specific connectivity network using metrics such as average shortest path length, network diameter, global clustering coefficient, network density, degree assortativity, attribute assortativity and the Integral Index of Connectivity (Coleman & Moré, 1983; Keeley et al., 2021; Minor & Urban, 2008; Newman, 2003; Pascual-Hortal & Saura, 2006; Watts & Strogatz, 1998). Regional metrics were used to compare scenarios, whereas local node strength metrics were used to identify where connectivity was concentrated within each landscape. Node strength measures the total weight of all realised dispersal connections associated with that cell.

The workflow from simulation output to network analysis was therefore:

Simulation outputs

- carrying capacity per grid cell;
- successful dispersal and settlement events.

Graph construction

- one graph created per map (2 per scenario)
- nodes: habitable cells and their carrying capacity obtained from the map with the highest carrying capacity
- edges: stored dispersal events (different per map)

Local and regional network analysis

- local node metrics calculated for each habitat node
- node strength used as the main indicator of the intensity of realised connection
- graph-level metrics calculated for each site and scenario;
- no-demonstrator, baseline and extended scenarios compared;

- IIC used as the main synthetic indicator of regional connectivity.

2.5 Construction of connectivity networks

Connectivity networks were constructed from the successful dispersal and settlement events recorded during the last 10% of the simulations. For each demonstrator and scenario, these events were converted into a graph in which habitat cells represented nodes and realised source–destination movements represented edges. The resulting networks therefore describe functional connectivity generated by the simulated arthropod community, rather than structural connectivity inferred from geographic proximity or habitat adjacency alone.

The model stores successful dispersal movements in sparse dispersal matrices, which were subsequently processed by the connectivity evaluation module. This module calculated local node-level and regional graph-level metrics, while the analysis module was used for exporting maps, tables and visualisations.

2.5.1 Successful dispersal events as network links

A dispersal event was included as a network link only when it occurred during the last 5 timesteps and when movement resulted in successful settlement in a suitable destination cell. Movements that ended outside the analysis domain or in cells with zero carrying capacity were excluded from the connectivity network.

A link between two cells therefore represents a realised movement from a source habitat cell to a destination habitat cell. Where multiple successful movements occurred between the same pair of cells, the connection was treated as stronger than a single realised event. Edge weights therefore represented the number or intensity of successful dispersal events between each source–destination pair. These weights were stored as raw counts representing the sum of all successful dispersal events across all species and considered timesteps. Due to coding restrictions and lack of relevance, not all network metrics were calculated using edge weights. Node strength was used as a local indicator of realised connectivity. It summarises the total weight of connections associated with a node and therefore identifies cells that function as local mobility hotspots within the simulated network.

2.5.2 Node and edge definition

For each scenario comparison, two graphs are constructed, one per map. To ensure comparability of graph metrics, both graphs share an identical node set. Each habitable cell is represented as a node. However, as the number of habitable cells may differ between the two maps within a comparison, the node set is determined by the map with the most habitable cells and the highest carrying capacity. For example, in the comparison between the baseline and no-demonstrator map, it is the baseline map that determines the set of nodes and their attributes, which include a unique identifier, spatial coordinates and carrying capacity. The node attributes are equal in both graphs, but the node metrics, such as strength, can differ since these are based on the graph edges which are map-specific Although both graphs use the same node set, the generational loops from which the edges emerge are based on the specific map being tested, including its unique set of habitable cells and carrying capacity values. Consequently, this results in different edge structures between graphs while maintaining an identical node set for comparability.

Edges represented realised dispersal connections between nodes. A directed edge from node *i* to node *j* indicated that at least one disperser moved from cell *i* to cell *j* and successfully settled there. Directionality was retained in the node-level analyses, as reflected by the calculation of in-closeness and out-closeness local metrics. As with edge weights, not all regional metrics account for directionality.

For interpretation, it is important to distinguish between the presence of habitat and its contribution to functional connectivity. A cell may have positive carrying capacity but contribute little to the realised network if it rarely sends or receives successful dispersers. Conversely, a cell with high node strength represents a location where many realised dispersal links originate, arrive or both.

2.5.3 Aggregation across species and timesteps

Connectivity networks were constructed at the community level by aggregating successful dispersal events across virtual species. This aggregation was necessary because the aim of D5.3 was to evaluate the connectivity response of each landscape for a trait-based arthropod community, rather than for a single focal species.

Aggregation across species combines movements generated by virtual species with different dispersal capacities and demographic strategies. More mobile species may contribute longer-distance links, whereas less mobile species depend more strongly on local stepping-stone structure. The resulting network therefore represents the combined realised mobility of the simulated virtual community.

Dispersal events were also aggregated across simulation timesteps before calculating scenario-level connectivity metrics. In the current analysis, events were pooled across the final **5** timesteps of the simulation, representing the realised set of functional links during the late or equilibrium phase of the model run. Regional metrics such as density, clustering, average shortest path length, diameter, assortativity and IIC were then calculated from the resulting scenario-specific networks.

The model includes several stochastic components, including the initial generation of the virtual species community. To ensure comparability between scenarios, the same random seed was used across all simulations, resulting in identical virtual communities for each scenario. Therefore, differences between scenarios can be attributed solely to changes in the landscape. Given this setup, replicate simulations were not included, as they would yield identical results under a fixed seed and thus not provide any additional information for comparing scenarios.

Definitions and ecological interpretations of all node- and network-level metrics are provided in **Appendix 2.5**. Regional metrics (Table 2.5.1) summarised the overall structure and integrated connectivity of each site, whereas local node metrics (Table 2.5.2) identified where realised movement was concentrated within the landscape.

Table 2.5.1. Regional (network-level) connectivity metrics

METRIC	WHAT IT MEASURES	ECOLOGICAL INTERPRETATION

INTEGRAL INDEX OF CONNECTIVITY (IIC)	Habitat availability accounting for habitat amount and connectivity	Synthetic measure of overall landscape connectivity; higher values indicate better functional integration of habitat.
NETWORK DENSITY	Proportion of possible links that are realised	Indicates the overall connectedness and redundancy of movement pathways.
GLOBAL CLUSTERING COEFFICIENT	Degree to which connected nodes form local clusters	Reflects local cohesion and the presence of stepping-stone neighbourhoods.
AVERAGE SHORTEST PATH LENGTH	Mean number of steps required to move between connected nodes	Lower values indicate more efficient movement through the network.
DIAMETER	Longest shortest path within the network	Indicates the maximum network distance and overall spatial extent of connectivity.
DEGREE ASSORTATIVITY	Tendency of nodes to connect to other nodes with similar degree	Describes network organisation, ranging from hub–periphery structures to highly connected cores.
ATTRIBUTE ASSORTATIVITY	Tendency of nodes with similar attributes (here: carrying capacity) to be connected	Indicates whether dispersal occurs mainly among similar or dissimilar habitat patches.
STRONG CONNECTIVITY INDICATOR	Whether all nodes are mutually reachable in the directed network	Indicates complete functional integration of the network.

References: Pascual-Hortal & Saura (2006); Urban & Keitt (2001); Minor & Urban (2008); Newman (2003); Watts & Strogatz (1998); Keeley et al. (2021).

Table 2.5.2. Local (node-level) connectivity metrics

METRIC	WHAT IT MEASURES	ECOLOGICAL INTERPRETATION
DEGREE CENTRALITY	Number of realised connections linked to a habitat cell	Identifies locally well-connected habitat patches that exchange dispersers with many other patches.
BETWEENNESS CENTRALITY	Frequency with which a node lies on shortest paths between other nodes	Identifies stepping-stone habitats that facilitate movement between otherwise disconnected parts of the network.
IN-CLOSENESS CENTRALITY	Ease with which a node can be reached from other nodes	Indicates how accessible a habitat patch is to incoming dispersers.
OUT-CLOSENESS CENTRALITY	Ease with which other nodes can be reached from a focal node	Indicates the potential of a habitat patch to act as a source of dispersers.
EIGENVECTOR CENTRALITY	Connectivity of a node weighted by the importance of its neighbours	Identifies habitat patches embedded within highly connected parts of the network.
CLUSTERING COEFFICIENT	Degree to which neighbouring nodes are interconnected	Reflects local network cohesion and redundancy of dispersal routes.
NODE STRENGTH	Sum of the weights of all realised dispersal links connected to a node	Measures the intensity of realised connectivity and identifies local mobility hotspots.

References: Urban & Keitt (2001); Minor & Urban (2008); Galpern et al. (2011); Newman (2003).

2.6 Statistical and comparative analyses

Connectivity responses were evaluated using paired scenario comparisons for each demonstrator site. Two contrasts were analysed: the local demonstrator effect, comparing the baseline scenario with the no-demonstrator scenario, and the extended-restoration effect, comparing the extended scenario with the corresponding baseline scenario.

Because connectivity networks now generated using a fixed random seed and identical node sets across all landscapes within a site, baseline networks are consistent across all scenarios. As a result, movement dynamics and the resulting graph structures for the baseline map are invariant, regardless of the scenario being evaluated. Differences among scenarios only arise in metrics that depend on carrying capacity, which is scenario-specific. Consequently, variation in baseline values is limited to metrics sensitive to these attributes—notably the Integral Index of Connectivity (IIC) and attribute assortativity—while all other network properties remain unchanged across contrasts.

For each network metric, scenario-specific values were extracted and compared within each site. We calculated the absolute difference between the two scenarios and, where available in the simulation output, the relative gain and relative loss. The resulting comparison table contained, for each site, contrast and metric, the starting value, final value, absolute change, relative gain and relative loss.

The analyses were primarily descriptive and comparative. Rather than estimating a single overall treatment effect, the objective was to assess how connectivity responses varied among demonstrators, scenarios and network metrics. This approach is appropriate because the demonstrators differ in coastal setting, surrounding habitat configuration, degree of urban fragmentation and scope for additional dune-front restoration.

2.6.1 Baseline versus no-demonstrator comparison

The baseline versus no-demonstrator comparison was used to quantify the realised contribution of the existing demonstrator. In this contrast, the no-demonstrator scenario was treated as the starting condition and the baseline scenario as the final condition. In the processed output table, this comparison was labelled local demonstrator effect.

For each metric M, the absolute local demonstrator effect was calculated as:

$$\Delta M_{\mathrm{local}} = M_{\mathrm{baseline}} - M_{\mathrm{no\ demo}}$$

where M_{baseline} is the metric value under the current demonstrator configuration and $M_{\text{no demo}}$ is the value under the no-demonstrator scenario.

Positive changes in IIC were interpreted as evidence that the existing demonstrator increased regional functional connectivity. Supporting metrics were used to identify whether this change reflected stronger local cohesion, increased link density, shorter movement pathways, network expansion or changes in network organisation.

2.6.2 Extended versus baseline comparison

The extended versus baseline comparison was used to quantify the additional connectivity gain associated with a more ambitious restoration configuration. In this contrast, the baseline scenario was treated as the starting condition and the extended restoration scenario as the final condition. In the processed output table, this comparison was labelled extended scenario.

For each metric M, the absolute extended-restoration effect was calculated as:

$$\Delta M_{\text{extended}} = M_{\text{extended}} - M_{\text{baseline}}$$

where M_{extended} is the metric value under the extended restoration scenario and M_{baseline} is the value under the corresponding baseline scenario.

Sites with large positive IIC changes under the extended scenario were interpreted as having high potential for additional regional connectivity gains. As in the local demonstrator comparison, relative gains were interpreted together with absolute changes and final IIC values, because sites with low initial connectivity can show large proportional responses even when final connectivity remains moderate.

2.6.3 Interpretation of relative gains

For each contrast, relative gain was used to express the proportional increase from the reference scenario to the improved scenario:

$$\text{Relative gain} = \frac{M_{\text{with}} - M_{\text{without}}}{M_{\text{without}}}$$

For the local demonstrator comparison, M_{with}corresponds to the baseline scenario and M_{without} to the no-demonstrator scenario. For the extended-restoration comparison, M_{with}corresponds to the extended scenario and M_{without} to the baseline scenario. Values were reported as percentages in the results tables and figures. Relative gain describes the proportional improvement compared with the starting scenario. Because relative gain depends on the initial value, it can be large when initial connectivity is low. Relative gains were therefore interpreted together with absolute metric values and absolute changes.

This distinction is particularly important for IIC. Sites with very low initial IIC may show large relative gains even when final IIC remains moderate or low. Conversely, sites with high initial IIC may show smaller relative gains because the network is already relatively well connected. For this reason, the results report both scenario-specific IIC values and relative IIC gains.

Not all metrics have the same ecological directionality. Increases in IIC, density and clustering generally indicate stronger connectivity or local cohesion. For average shortest path length and diameter, lower values may indicate more efficient movement, but higher values may indicate network expansion. Assortativity metrics describe network organisation and were not interpreted as inherently positive or negative. Restoration performance was therefore assessed primarily using IIC, while the other metrics were used to explain the structural mechanisms behind changes in regional connectivity.

2.6.4 Relationship between initial connectivity and restoration gain

To assess whether restoration responses depended on the initial state of the network, we analysed the relationship between initial IIC and restoration gain. For the local demonstrator comparison, initial connectivity was defined as the IIC value in the no-demonstrator scenario. For the extended-restoration comparison, it was defined as the IIC value in the baseline scenario.

Two response variables were considered:

- absolute IIC change, calculated as the difference between final and initial IIC;
- relative IIC gain, calculated as the proportional increase relative to the initial scenario.

Absolute and relative gains were analysed separately because they describe different aspects of restoration response. Absolute gain measures the total increase in functional connectivity, whereas relative gain measures the proportional improvement from the starting condition. Sites with very low initial IIC may therefore show large relative gains even if their final connectivity remains lower than that of more connected sites.

Relationships between initial IIC and restoration gain were evaluated separately for the local demonstrator effect and the extended-restoration effect. A pooled exploratory analysis across both comparison types was also used to assess general tendencies. Spearman rank correlations were used to assess monotonic relationships less sensitive to non-normality and extreme values. Given the limited number of demonstrator sites, these correlations were interpreted as exploratory rather than as formal hypothesis tests.

The expectation was that sites with lower initial connectivity would show greater proportional restoration potential, particularly under the extended-restoration scenario. However, absolute gains may also depend on the amount and spatial position of added habitat, the structure of the surrounding dune network and whether restored habitat bridges existing gaps or mainly expands already connected areas. Restoration performance was therefore interpreted using initial IIC, final IIC, absolute change and relative gain together.

3. Model outputs and connectivity responses

Regional connectivity outputs were generated for 11 DuneFront demonstrator sites. We first compare cross-site patterns in the Integral Index of Connectivity (IIC) to assess the realised contribution of existing demonstrators and the potential added value of extended dune-front restoration. We then use supporting network metrics to clarify whether changes in IIC reflect denser linkage among habitat cells, stronger local clustering, altered path structure, network expansion or changes in network organisation. Site-level interpretations are presented in Section 4.

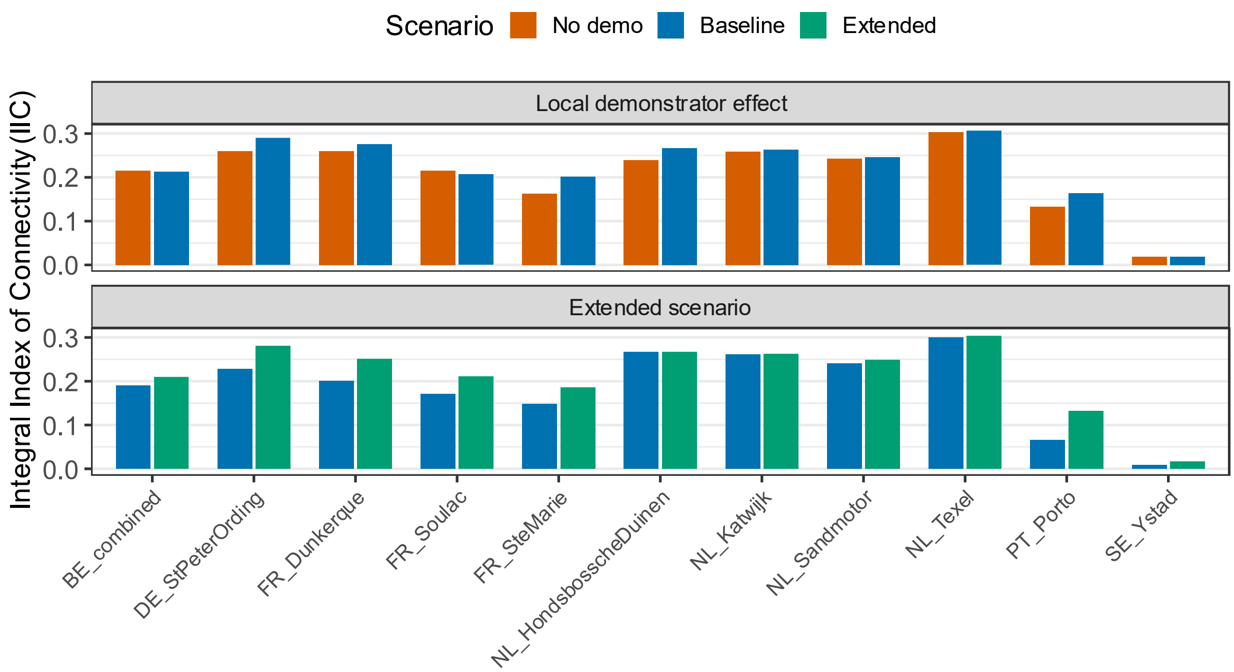


***Figure 3.0. Integral Index of Connectivity across restoration scenarios.** Overview of the realised **Integral Index of Connectivity (IIC)** for each demonstrator site under the no-demonstrator, baseline demonstrator and extended restoration scenarios. The no-demonstrator and baseline scenarios are used to quantify the local effect of the existing demonstrator, whereas the extended scenario represents the potential connectivity gain of a broader dune-in-front-of-dike restoration configuration where this was applicable within the regional coastal network. Baseline values differ between comparisons because IIC is calculated using the node set and carrying-capacity representation specific to each scenario comparison.*

3.1 Local demonstrator effects: baseline versus no-demonstrator

The baseline scenario showed higher IIC than the no-demonstrator scenario for almost all analysed sites, indicating that the existing DuneFront demonstrators mostly contributed positively to regional functional connectivity. However, the magnitude of this contribution varied strongly among sites, with three sites even showing a decrease in IIC. These sites are BE_combined, FR_Soulac, and SE_Ystad.

Table 3.2. Local demonstrator effect on regional IIC. Values show IIC in the no-demonstrator and baseline scenarios, the absolute difference between both scenarios, and the relative IIC gain.

Site	*IIC no-demonstrator*	*IIC baseline*	*Absolute IIC change*	*Relative IIC gain (%)*
BE_combined	0.215	0.213	-0.002	-0.83
DE_StPeterOrding	0.260	0.290	0.030	11.6
FR_Dunkerque	0.260	0.276	0.016	6.0
FR_Soulac	0.215	0.207	-0.009	-4.0
FR_SteMarie	0.163	0.202	0.039	24.1
NL_HondsbosscheDuinen	0.240	0.266	0.027	11.2
NL_Katwijk	0.258	0.263	0.004	1.7
NL_Sandmotor	0.243	0.246	0.003	1.3
NL_Texel	0.303	0.306	0.003	1.0
PT_Porto	0.133	0.164	0.031	23.4
SE_Ystad	0.0193	0.0190	-0.0003	-1.4

The strongest proportional response occurred at FR_SteMarie, where IIC increased from 0.163 to 0.202. PT_Porto showed a comparable increase (+23.4%), while substantial positive effects were also observed for DE_StPeterOrding and NL_HondsbosscheDuinen (11.2–11.6%). These pronounced gains indicate that the added habitat is strategically positioned within the network, effectively strengthening connections between existing patches, shortening path lengths, or increasing the number of reachable pairs.

FR_Dunkerque, NL_Katwijk, NL_Sandmotor, and NL_Texel showed smaller, though still positive, responses (≤ 6%). This suggests that the added habitat provides only limited improvements to network structure, either because it contributes few additional links or because it is embedded in already well-connected systems where most shortest paths and functional connections are already established.

In contrast, negative responses were observed at BE_combined, FR_Soulac, and SE_Ystad (-4.0% to -0.83%). At these sites, the demonstrators are relatively small and appear to introduce weakly connected or functionally isolated patches, often lying beyond key dispersal thresholds or linking only through low-weight connections. As a result, they contribute little to shortest-path structure or the number of reachable pairs, while still increasing total habitat area. This leads to a dilution effect in the IIC metric, highlighting that increases in habitat amount do not necessarily translate into improved connectivity, and that spatial placement relative to the existing network structure is critical

Overall, the local demonstrator comparison shows that existing DuneFront interventions generally enhance regional connectivity, but not to the same degree everywhere (Figure 3.1). The largest gains occurred where the demonstrator was positioned to improve network integration, whereas sites embedded in already relatively connected landscapes showed more modest proportional responses. This indicates that the connectivity value of a dune-front intervention depends not only on the amount of habitat added, but also on its position within the wider coastal network. The ranking of relative gains (Figure 3.2) highlights the contrast between sites where the current demonstrator acts as a regional connector and sites where its contribution is mainly incremental.

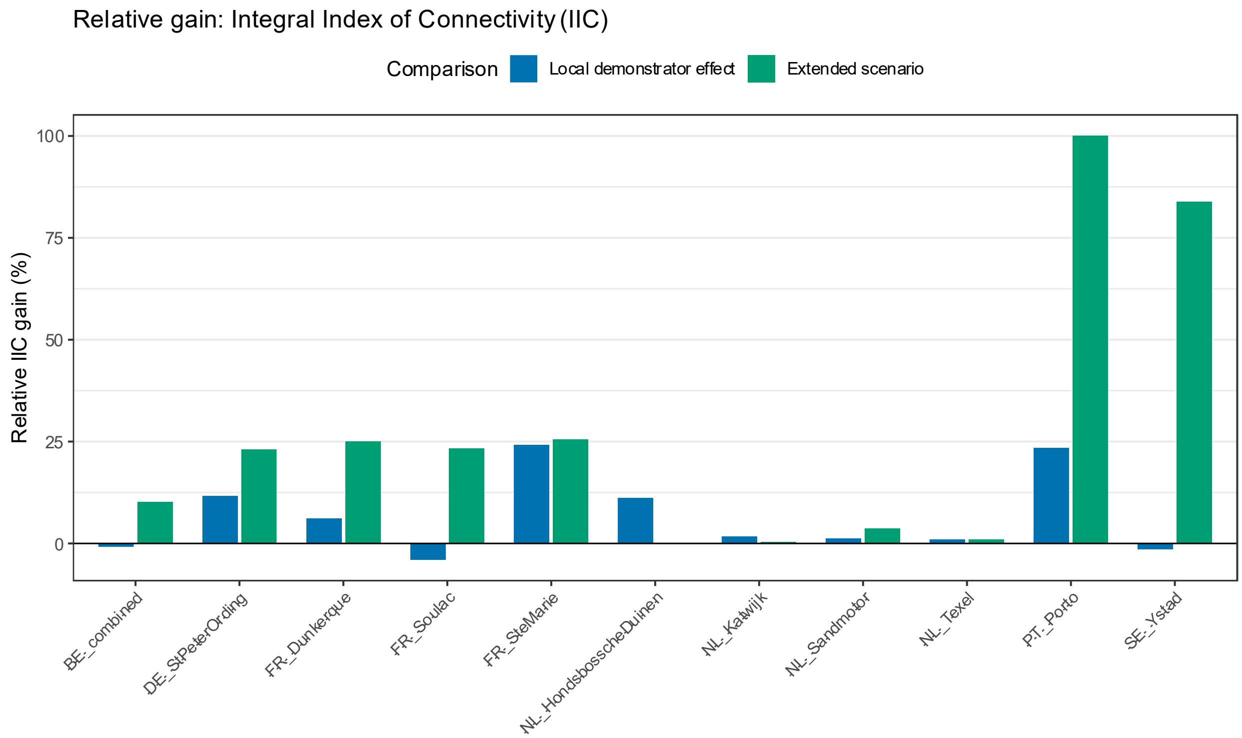


***Figure 3.1. Relative IIC gain of existing demonstrators.** Relative gain in the **Integral Index of Connectivity (IIC)** for the baseline demonstrator scenario compared with the no-demonstrator scenario, and for the extended scenario compared to the baseline. The figure shows the realised local connectivity contribution of each existing demonstrator, with higher values indicating stronger proportional improvement in regional functional connectivity relative to the counterfactual situation without the demonstrator.*

3.2 Extended restoration effects: extended versus baseline

The extended restoration comparison assessed the additional connectivity gain that could be achieved by expanding dune-front restoration beyond the current demonstrator configuration. Across most sites, the extended scenario increased IIC relative to baseline, but the magnitude of this response varied strongly. Relative gains ranged from no additional increase in NL_HondsbosscheDuinen to 100% in PT_Porto.

Table 3.3. Extended restoration effect on regional IIC. Values show IIC in the baseline and extended scenarios, the absolute difference between both scenarios, and the relative IIC gain.

Site	*IIC baseline*	*IIC extended*	*Absolute IIC change*	*Relative IIC gain (%)*
BE_combined	0.191	0.210	0.019	10.1
DE_StPeterOrding	0.228	0.280	0.053	23.1
FR_Dunkerque	0.200	0.251	0.050	25.0
FR_Soulac	0.171	0.211	0.040	23.3
FR_SteMarie	0.148	0.186	0.038	25.5
NL_HondsbosscheDuinen	0.266	0.266	0.000	0.0
NL_Katwijk	0.261	0.262	0.001	0.3
NL_Sandmotor	0.240	0.249	0.009	3.6
NL_Texel	0.300	0.303	0.003	1.0
PT_Porto	0.066	0.132	0.066	100.0
SE_Ystad	0.009	0.017	0.008	83.8

The largest proportional response occurred at PT_Porto, where IIC increased from 0.066 to 0.132, corresponding to a relative gain of 100%. SE_Ystad showed also a high relative gain of 83.8%, although its final IIC remained low in absolute terms.

Strong extended-restoration effects were also observed for FR_SteMarie, FR_Dunkerque, FR_Soulac, and DE_StPeterOrding, with relative gains of 25.5%, 25.0%, 23.3%, and 23.1 respectively. These sites appear to have substantial unrealised potential for regional connectivity restoration, most likely because additional dune habitat is positioned where it can close gaps or strengthen links among existing habitat patches.

A more moderate gain was found for BE_combined, with a relative increase of 10.1%. For NL_Sandmotor and NL_Texel, small gains of 3.6% and 1.0% were recorded, respectively. NL_Katwijk showed an even smaller additional increase of 0.3%, while NL_HondsbosscheDuinen showed no change because the extended scenario did not differ from the baseline in the available model output.

Overall, the extended scenario produced stronger and more variable responses than the local demonstrator comparison (Figure 3.2). The largest gains occurred in sites where additional dune habitat could substantially alter the spatial organisation of the regional network, rather than simply enlarge an already connected system. PT_Porto, FR_SteMarie, FR_Dunkerque, DE_StPeterOrding, and FR_Soulac therefore emerge as high-potential systems for scaled-up dune-front restoration. In contrast, NL_Katwijk and NL_HondsbosscheDuinen showed limited additional gain under the scenario tested.

Large proportional gains should nevertheless be interpreted alongside absolute IIC values. This is particularly relevant for SE_Ystad, where the relative response was high but final connectivity remained low. By contrast, FR_Dunkerque and FR_SteMarie combined large relative gains with substantial absolute increases, indicating both high responsiveness and meaningful improvement in regional connectivity.

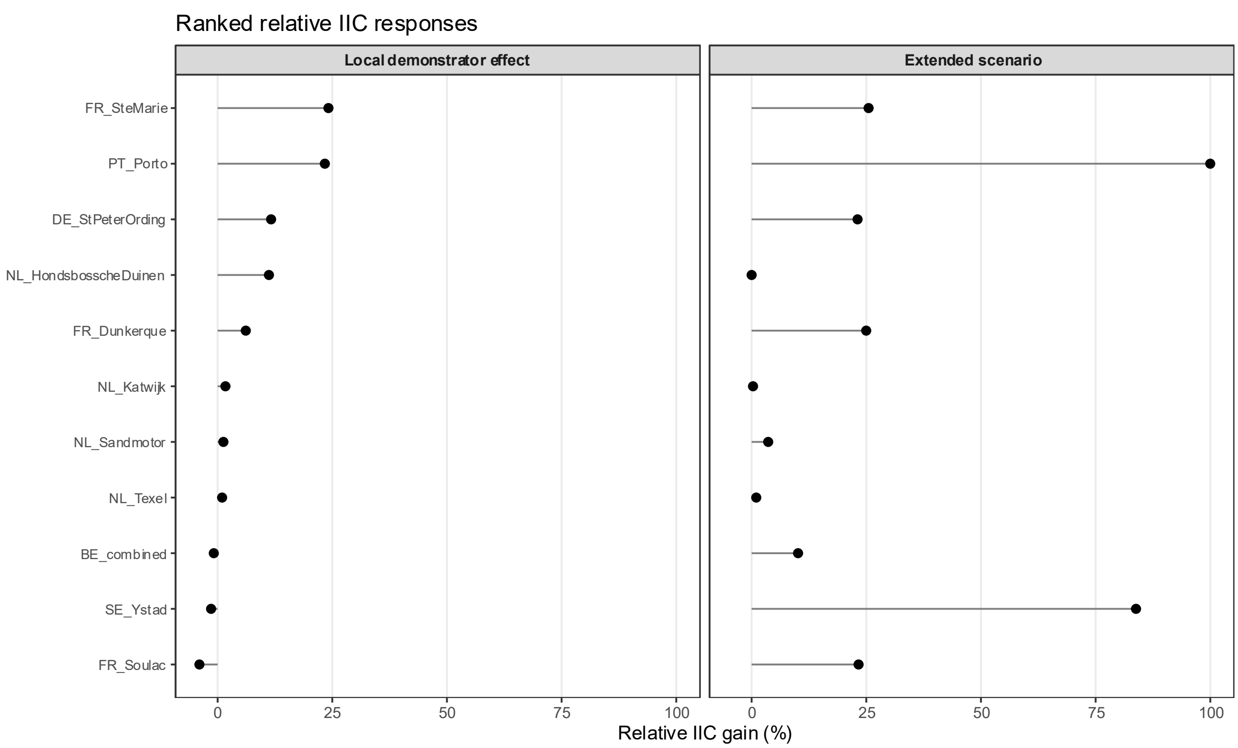


Figure 3.2. Relative IIC responses across demonstrator sites, ranked according to local demonstrator effects. *Relative gain in the Integral Index of Connectivity (IIC) for each demonstrator site, shown separately for the local demonstrator effect and the extended restoration scenario. Sites are ordered by relative gain to highlight differences between connectivity benefits already delivered by existing demonstrators and additional gains projected under extended restoration. Large proportional gains should be interpreted together with absolute IIC values, because low initial connectivity can produce high relative responses even when final connectivity remains limited.*

3.3 Cross-site variation in network structure

Changes in IIC provide the main synthetic measure of regional functional connectivity, but the supporting network metrics clarify how connectivity changed between scenarios. Across sites, increases in IIC were often accompanied by changes in density, clustering, path-based metrics and assortativity, indicating that similar IIC responses can arise through different structural mechanisms. Full values for these supporting metrics are provided in Appendix 3.3.

For the local demonstrator effect PT_Porto and DE_STPeterOrding showed the clearest improvement in network efficiency. In both sites, the baseline scenario increased IIC relative to the no-demonstrator scenario while also increasing density and clustering, and reducing average shortest path length and diameter. This pattern indicates that the existing demonstrator did more than add habitat: it shortened movement pathways and strengthened the internal organisation of the regional network.

A different pattern was observed in sites such as FR_SteMarie and NL_HondsbosscheDuinen. Here, IIC increased while path-based metrics increased or remained broadly stable. These responses are consistent with network expansion rather than reduced connectivity. In such cases, the demonstrator appears to add or integrate habitat nodes across a larger spatial extent, increasing total connected habitat even if some nodes become separated by more network steps.

Extended restoration produced particularly strong structural responses in several sites. In FR_Dunkerque, FR_SteMarie, PT_Porto and SE_Ystad, increases in IIC were accompanied by clear changes in density and/or clustering, indicating that additional dune habitat created new realised links and strengthened local network cohesion. In FR_Soulac, the extended scenario also reduced average shortest path length and diameter, suggesting a particularly favourable response in which restoration both increased overall connectivity and improved movement efficiency.

In other extended scenarios, notably FR_Dunkerque, FR_SteMarie, PT_Porto and SE_Ystad, IIC increased together with average shortest path length and diameter. This pattern reflects the addition of habitat across a broader spatial extent. Longer paths in these cases should therefore be interpreted as a signal of network expansion, not as evidence of reduced functional connectivity.

Assortativity responses were more heterogeneous. Degree assortativity increased in several extended scenarios, including DE_StPeterOrding, FR_Dunkerque, FR_Soulac, FR_SteMarie, NL_Sandmotor, NL_Texel and PT_Porto, suggesting that restoration often reinforced connections among nodes with similar numbers of links or strengthened more organised network cores. Decreases in degree assortativity, as observed for NL_Katwijk and SE_Ystad, point instead to a more hub–periphery structure, where central nodes become linked to less connected peripheral habitat cells.

Attribute assortativity generally increased, although the magnitude of change varied across sites. Increases, such as those observed for DE_StPeterOrding and FR_Dunkerque under the extended scenario, suggest stronger linkage among similar habitat or node types. Decreases, only observed for SE_Ystad, may indicate that restoration created links across more heterogeneous habitat elements. Because both patterns can be ecologically meaningful, assortativity was interpreted as a descriptor of network organisation rather than as a direct measure of restoration success.

None of the simulated regional networks became strongly connected under any scenario. Thus, although demonstrators and extended restoration generally improved network integration, they did not remove all directional or structural fragmentation at the analysed scale. The restoration scenarios should therefore be interpreted as strengthening stepping-stone function and regional integration, rather than producing complete mutual reachability among all habitat nodes.

Together, these metrics show that IIC gains were generated through different mechanisms across sites (Table 3.4). Some demonstrators improved network efficiency by shortening movement pathways, whereas others expanded the connected habitat network across a larger coastal extent. Supporting metrics are therefore essential for distinguishing between denser local linkage, shorter routes, network expansion and broader changes in network organisation.

Table 3.4. Summary interpretation of supporting network metric responses.

Metric response pattern	*Ecological interpretation*	*Example sites*

IIC increases, density/clustering increase, path length decreases	Restoration improves both total connectivity and movement efficiency	PT_Porto local effect; DE_StPeterOrding local effect; FR_Soulac extended scenario
IIC increases, path length/diameter increase	Restoration expands the network by adding habitat nodes across a larger spatial extent	BE_combined extended scenario; FR_Dunkerque extended scenario; FR_SteMarie local and extended effects; SE_Ystad extended scenario
IIC increases, assortativity decreases	Restoration may connect different node types or link peripheral habitat to network cores	SE_Ystad extended scenario
IIC stable, supporting metrics stable	Scenario does not substantially change the network configuration	NL_HondsbosscheDuinen extended scenario

3.4 Relationship between initial connectivity and restoration gain

Restoration responses were partly related to the initial connectivity of each regional network. Initial connectivity was defined as the IIC value in the starting scenario: the no-demonstrator scenario for the local demonstrator comparison, and the baseline scenario for the extended-restoration comparison. Restoration gain was evaluated as both absolute IIC change and relative IIC gain.

The clearest pattern occurred for the extended-restoration scenarios. Sites with lower initial IIC tended to show larger proportional gains, with a strong negative relationship between initial IIC and relative IIC gain. This relationship was supported by Spearman rank correlation, $\rho = -0.918$. The largest relative gains were observed in sites with low baseline connectivity, including PT_Porto and SE_Ystad. PT_Porto increased from 0.066 to 0.132 under the extended scenario, corresponding to a relative gain of 100.0%, while SE_Ystad increased from 0.009 to 0.017, corresponding to 83.8%. By contrast, sites with higher initial IIC, such as NL_HondsbosscheDuinen, NL_Katwijk and NL_Texel, showed smaller relative gains.

The same tendency was less pronounced for the local demonstrator comparison. This indicates that the realised effect of existing demonstrators is less consistently determined by initial network connectivity alone. Local demonstrators can produce substantial gains when they are strategically positioned, but their effect also depends on the spatial arrangement of surrounding habitat and whether the intervention bridges existing network discontinuities.

Absolute and relative gains provided complementary information. Several initially fragmented sites showed large proportional responses, but this did not always translate into high final connectivity. SE_Ystad, for example, had a high relative gain under the extended scenario but remained low in absolute IIC. In contrast, FR_Dunkerque and FR_SteMarie combined large relative gains with substantial absolute increases, indicating both high responsiveness and a meaningful improvement in regional connectivity.

Overall, extended dune-front restoration showed the greatest proportional potential in initially fragmented coastal landscapes. This supports the interpretation of restored dune habitats as stepping stones in sparse or discontinuous networks. However, restoration potential should not be assessed from relative gain alone. Initial IIC, final IIC, absolute change and relative gain need to be considered together to distinguish large proportional responses from changes that also lead to high final connectivity.

3.5 Summary of key response types

Connectivity responses differed markedly among demonstrator sites. To summarise this variation, sites were grouped into broad response types based primarily on IIC responses, with supporting information from density, clustering, path-based metrics and assortativity. The typology is intended as an interpretive synthesis rather than a formal clustering analysis, and the response types are not mutually exclusive. Some sites therefore appear in more than one category.

Table 3.6. Connectivity-response typology of DuneFront demonstrator sites.

Response type	*Description*	*Example sites*	*Interpretation*
Strong current demonstrator effect	Existing demonstrator already produces a large positive IIC gain relative to the no-demonstrator scenario	PT_Porto, DE_StPeterOrding, FR_SteMarie, NL_HondsbosscheDuinen	Current intervention functions as an important regional connectivity node or stepping stone

High extended-restoration potential	Extended scenario produces large additional IIC gain relative to baseline	PT_Porto, FR_SteMarie, SE_Ystad, FR_Dunkerque, FR_Soulac, DE_SPeterOrding	Scaling up restoration could substantially improve regional functional connectivity
Moderate but consistent response	Both local and extended effects are positive, but gains are not transformative	NL_Sandmotor, NL_Texel	Restoration contributes positively, but the network is not strongly reorganised
Limited additional restoration gain	Extended scenario adds little or no connectivity benefit relative to baseline	NL_HondsbosscheDuinen, NL_Katwijk	Existing configuration may already capture most achievable connectivity gains, or the tested extension does not close major network gaps
Low absolute but high relative sensitivity	Relative gain is large because initial IIC is very low, but final IIC remains comparatively low	SE_Ystad, BE_combined,	Restoration improves connectivity proportionally, but regional isolation remains important

The typology highlights three main patterns. First, several existing demonstrators already make a substantial contribution to regional connectivity. This was clearest for PT_Porto and FR_SteMarie, and also evident for DE_StPeterOrding and NL_HondsbosscheDuinen. These sites show that current dune-front configurations can function as effective stepping stones when they are positioned in locations that improve network integration.

Second, several sites showed high additional potential under the extended restoration scenario. PT_Porto, FR_SteMarie, FR_Dunkerque, DE_StPeterOrding and FR_Soulac combined large relative gains with meaningful increases in IIC, suggesting that additional dune habitat could strengthen regional connectivity. SE_Ystad also showed a large proportional response, but its final IIC remained low, indicating that restoration improves connectivity from a very fragmented starting point without fully overcoming regional isolation.

Third, some sites showed more limited additional gains. NL_HondsbosscheDuinen showed no difference between the baseline and extended scenarios in the available model output, while NL_Katwijk and NL_Texel showed only a small increase. These cases suggest that the current configuration already captures much of the potential connectivity benefit and that the tested extension does not add habitat in locations that substantially alter the regional network.

Overall, the typology shows that DuneFront demonstrators can improve connectivity through different pathways. In some sites, existing interventions already act as regional connectors. In others, the main opportunity lies in scaling up restoration to close larger network gaps. In more connected or spatially constrained systems, additional restoration may produce smaller gains, and biodiversity benefits may depend more on habitat quality, successional diversity or local management than on further expansion alone.

4. Demonstrator-level connectivity

The regional metrics presented in Section 3 summarise how each demonstrator affects functional connectivity at the scale of the surrounding coastal network. Here, these results are complemented with local node-strength maps for the no-demonstrator, baseline and extended restoration scenarios. Node strength was selected because it summarises the total intensity of realised dispersal connections associated with each habitat node. The maps therefore indicate where simulated movement is concentrated within each landscape and help distinguish between demonstrators that mainly add local habitat, reinforce existing mobility hotspots or act as stepping stones between neighbouring habitat areas. The site-level interpretations combine regional IIC responses with local node-strength patterns to provide a concise assessment of each demonstrator.

Maps show local node strength for the no-demonstrator, baseline and extended restoration scenarios. Node strength represents the total intensity of realised dispersal connections associated with each habitat node; higher values indicate stronger participation in the simulated connectivity network.

4.1 BE_combined

For the Belgian combined demonstrator area, the local demonstrator effect was negative. IIC decreased from 0.215 in the no-demonstrator scenario to 0.213 in the baseline scenario, corresponding to a relative change of -0.83%. This decrease was accompanied by a slight increase in clustering, while network density remained constant. In addition, average shortest path length and network diameter increased. Together, these changes suggest that the current demonstrator does not enhance regional connectivity and may instead add habitat nodes without improving overall network cohesion. The extended scenario does increase the IIC from 0.191 to 0.210, corresponding to a relative gain of 10.1%. In this case, both clustering and density increased more clearly, while path length and diameter also increased, indicating a combination of stronger local cohesion and expansion of the alongshore network. In addition to strengthening local connectivity within existing dune clusters, the extended scenario increases alongshore connectivity in the central coastal sections near Ostend.

Overall, BE_combined does not show a current demonstrator effect. However, the extended scenario appears to function as a connector of existing urban dune complexes, with high additional potential under extended restoration. The supporting metrics suggest that this effect reflects both network expansion and increased local cohesion along a highly urbanised coast.

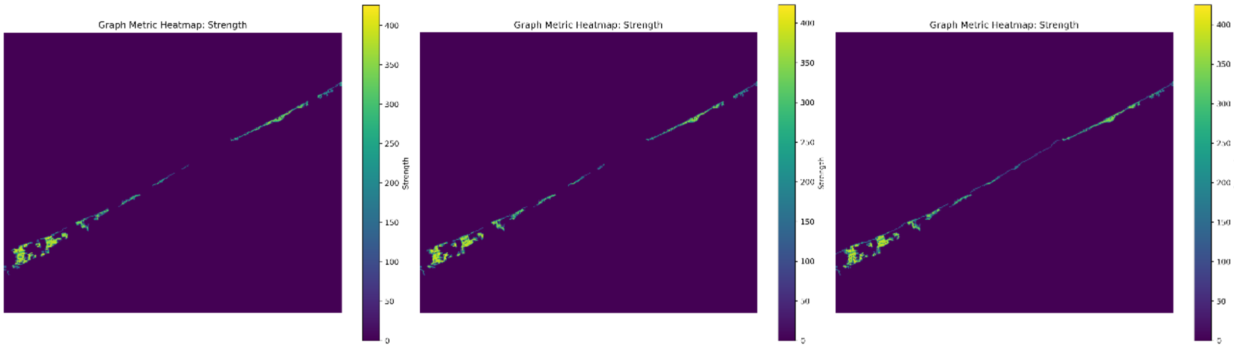


Figure 4.1. Local node strength across restoration scenarios for the Belgian combined site. *Maps show the no-demonstrator, baseline and extended restoration scenarios. Higher values indicate nodes that participate more strongly in successful dispersal connections.*

4.2 DE_StPeterOrding

DE_StPeterOrding showed a substantial positive local demonstrator effect. IIC increased from 0.260 in the no-demonstrator scenario to 0.290 in the baseline scenario, corresponding to a relative gain of 11.6%. In contrast to several other sites, this IIC increase was accompanied by a decrease in average shortest path length and diameter, together with increases in density and clustering. This indicates a clear connecting effect: the existing demonstrator not only adds habitat to the network, but also makes movement pathways more efficient. The extended scenario further increased IIC from 0.228 to 0.280, corresponding to a relative gain of 23.1%. However, under the extended scenario, average shortest path length and diameter increased, while density and clustering also increased. This suggests that extended restoration mainly expands the connected network while also strengthening local cohesion. This pattern is visible in Figure 4.2, particularly in the potential restoration.

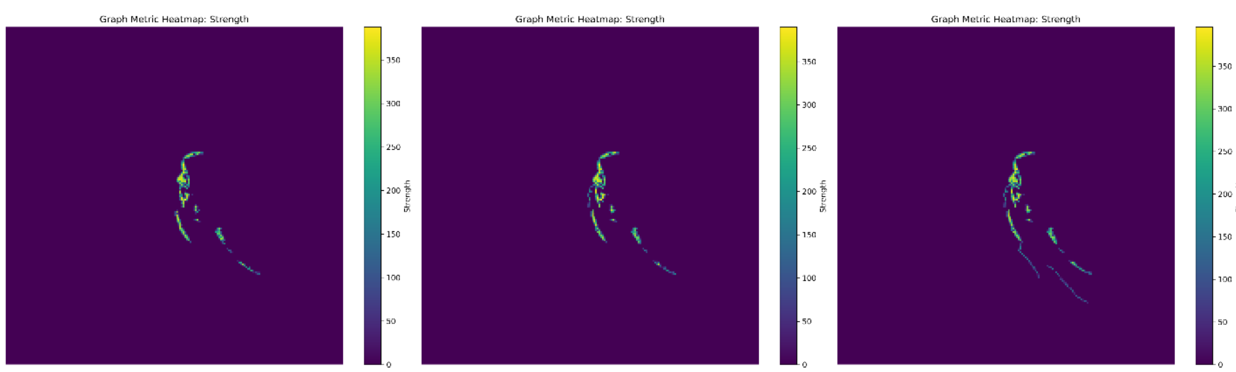


Figure 4.2. Local node strength across restoration scenarios for the St Peter Ording site. *Maps show the no-demonstrator, baseline and extended restoration scenarios. Higher values indicate nodes that participate more strongly in successful dispersal connections.*

Overall, DE_StPeterOrding shows a strong realised demonstrator effect. The strength maps show that the existing demonstrator already functions as an important local mobility hub, with extended restoration providing additional but more expansion-oriented connectivity benefits.

4.3 FR_Dunkerque

The local demonstrator effect at FR_Dunkerque was relatively small. IIC increased from 0.260 in the no-demonstrator scenario to 0.276 in the baseline scenario, corresponding to a relative gain of 6.0%. Supporting metrics confirm that this is a limited structural change: density, clustering, and average shortest path length increased only slightly, and diameter remained unchanged. This suggests that the current demonstrator adds local habitat value but does not substantially reorganise the regional network. In contrast, the extended scenario produced a much stronger response, with IIC increasing from 0.200 to 0.251, corresponding to a relative gain of 25.0%. This was accompanied by an increase in density and clustering, but also by large increases in average shortest path length and diameter. The extended scenario therefore appears to expand the network substantially, connecting larger dune complexes to the east while also extending the network westwards (Figure 4.3).

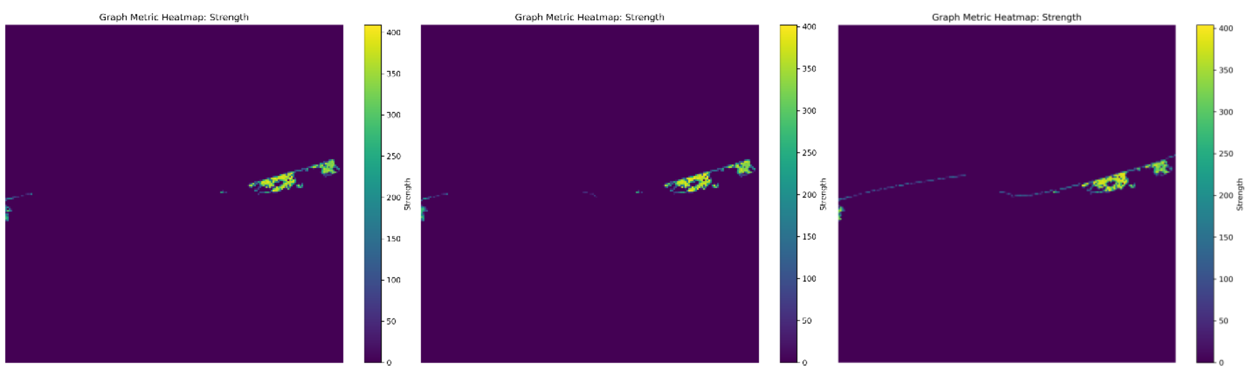


Figure 4.3. Local node strength across restoration scenarios for the Dunkerque site. *Maps show the no-demonstrator, baseline and extended restoration scenarios. Higher values indicate nodes that participate more strongly in successful dispersal connections.*

Overall, FR_Dunkerque shows limited realised connectivity gain under the current demonstrator configuration, but substantial potential for network expansion and regional integration under extended dune-front restoration.

4.4 FR_Soulac

The local demonstrator effect at FR_Soulac was relatively small but negative. IIC decreased from 0.215 in the no-demonstrator scenario to 0.207 in the baseline scenario, corresponding to a relative gain of -4.0%. This was accompanied by small increases in density and clustering, but also by increases in average shortest path length and diameter. This suggests that the current demonstrator mainly expands or adds to the network without improving movement efficiency. The extended scenario produced a much stronger effect, increasing IIC from 0.171 to 0.211, corresponding to a relative gain of 23.3%. In contrast to the local comparison, the extended scenario increased density and clustering while reducing both average shortest path length and diameter. This points to a strong connecting effect: extended restoration not only adds habitat but also improves the efficiency of movement through the network.

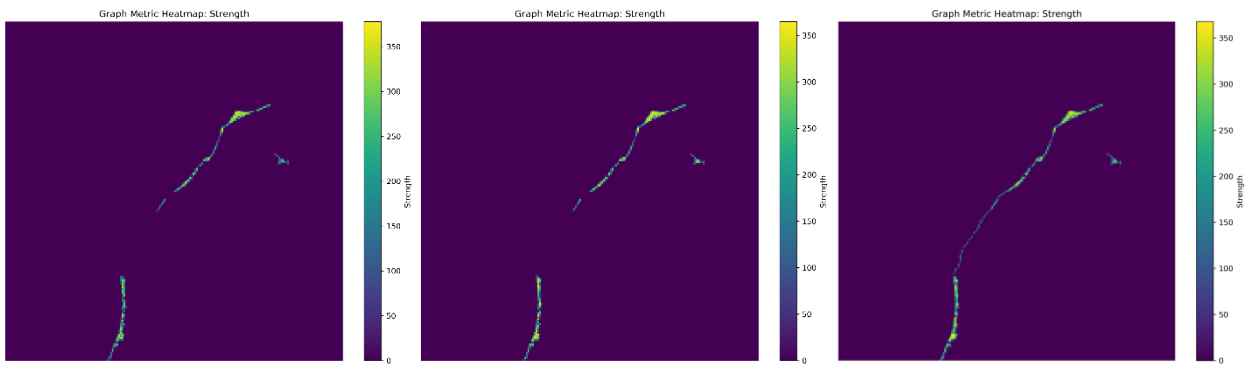


Figure 4.4. Local node strength across restoration scenarios for the Soulac site. *Maps show the no-demonstrator, baseline and extended restoration scenarios. Higher values indicate nodes that participate more strongly in successful dispersal connections.*

Overall, FR_Soulac shows currently a loss in connectivity, but substantial potential under extended restoration. The supporting metrics suggest that scaling up restoration could not only add habitat to the network but also improve movement efficiency across the system.

4.5 FR_SteMarie

FR_SteMarie showed a strong local demonstrator effect. IIC increased from 0.163 in the no-demonstrator scenario to 0.202 in the baseline scenario, corresponding to a relative gain of 24.1%. Density and clustering increased slightly, but average shortest path length and diameter also increased. This suggests that the local demonstrator improves overall habitat-network integration, but mainly by adding or extending connected habitat rather than by shortening routes. The extended scenario also produced a strong response, increasing IIC from 0.148 to 0.186, corresponding to a relative gain of 25.5%. This was accompanied by a marked increase in clustering and a moderate increase in density, alongside increases in path length and diameter. The extended scenario therefore appears to create a much larger and more cohesive network, although one that also spans a greater spatial extent.

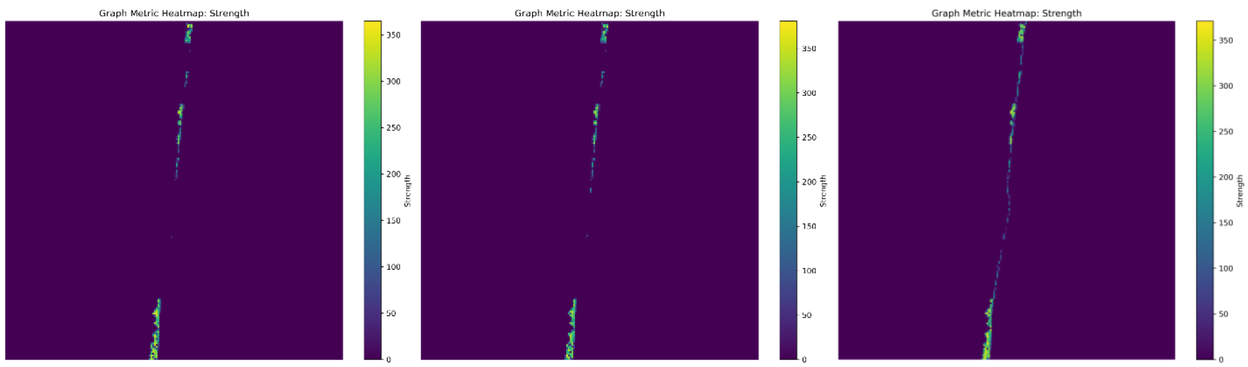


Figure 4.5. Local node strength across restoration scenarios for the Ste Marie site. *Maps show the no-demonstrator, baseline and extended restoration scenarios. Higher values indicate nodes that participate more strongly in successful dispersal connections.*

Overall, FR_SteMarie shows both a strong current demonstrator effect and a high extended-restoration potential. The supporting metrics indicate that the extended scenario combines network expansion with increased local cohesion, making FR_SteMarie one of the clearest high-response sites in the analysis.

4.6 NL_HondsbosscheDuinen

NL_HondsbosscheDuinen showed a substantial local demonstrator effect. IIC increased from 0.240 in the no-demonstrator scenario to 0.266 in the baseline scenario, corresponding to a relative gain of 11.2%. Unlike sites where IIC gains were associated with large increases in path length or diameter, the path-based metrics changed very little: average shortest path length increased only marginally and diameter remained unchanged. At the same time, density, clustering and assortativity increased. This suggests that the demonstrator improves connectivity mainly by strengthening local cohesion and network organisation rather than by expanding the spatial extent of the network. The extended scenario was identical to the baseline in the simulation output, indicating that the tested restoration objective was already represented by the current demonstrator configuration. As a result, no additional IIC gain or structural change was observed.

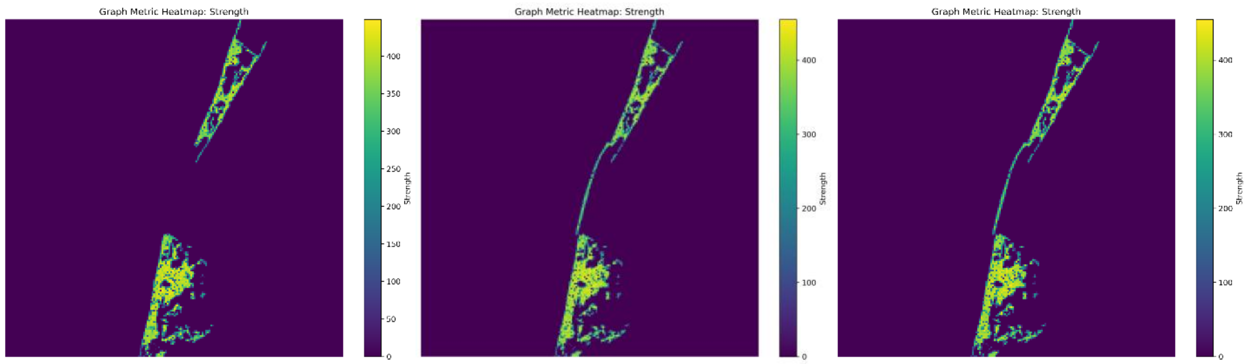


Figure 4.6. Local node strength across restoration scenarios for the Hondsbossche duinen site. *Maps show the no-demonstrator, baseline and extended restoration scenarios. Higher values indicate nodes that participate more strongly in successful dispersal connections.*

Overall, NL_HondsbosscheDuinen provides a strong realised connectivity benefit under the current configuration. The tested extended scenario did not add further connectivity value because it did not differ from the baseline representation.

4.7 NL_Katwijk

NL_Katwijk showed a small local demonstrator effect. IIC increased from 0.258 in the no-demonstrator scenario to 0.263 in the baseline scenario, corresponding to a relative gain of 1.7%. Supporting metrics show only minor structural change: density increased slightly, diameter remained unchanged, average path length changed little, and clustering decreased slightly. This suggests that the IIC gain reflects additional habitat availability or local integration rather than a major reorganisation of the network. The extended scenario produced only a very small additional increase, with IIC rising from 0.261 to 0.262, corresponding to a relative gain of 0.3%. Density, clustering, and path length increased only slightly, while diameter remained unchanged.

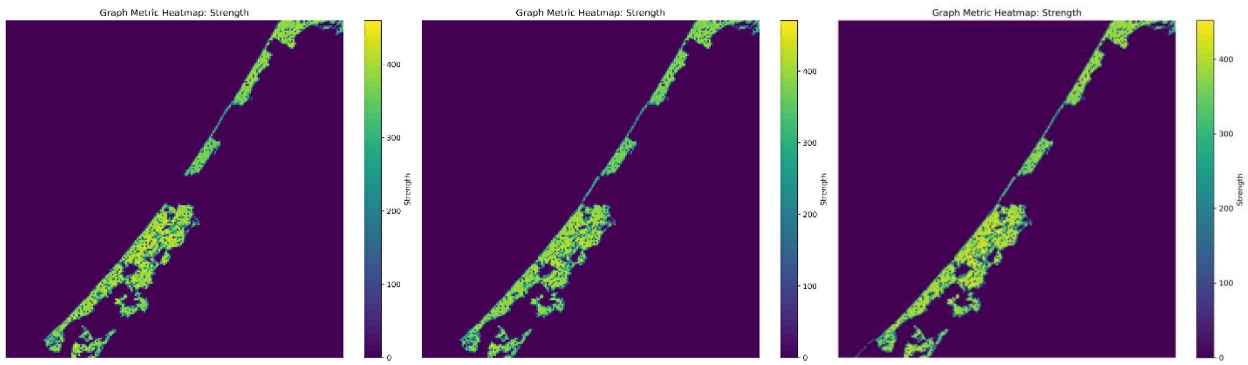


Figure 4.7. Local node strength across restoration scenarios for the Katwijk site. *Maps show the no-demonstrator, baseline and extended restoration scenarios. Higher values indicate nodes that participate more strongly in successful dispersal connections.*

Overall, NL_Katwijk shows a small current demonstrator effect with limited additional gain under the extended scenario. The tested extension does not substantially alter regional network structure, suggesting that the baseline configuration already captures most of the connectivity benefit represented in this scenario.

4.8 NL_Sandmotor

The local demonstrator effect at NL_Sandmotor was low. IIC increased from 0.243 in the no-demonstrator scenario to 0.246 in the baseline scenario, corresponding to a relative gain of 1.3%. This was accompanied by increases in density and clustering, while diameter remained unchanged and average path length increased. This suggests that the current demonstrator strengthens local cohesion and link density, although it does not strongly shorten movement routes. Under the extended scenario, IIC increased from 0.240 to 0.249, corresponding to an additional relative gain of 3.6%. In this comparison, average path length decreased slightly, diameter remained unchanged, density and clustering increased slightly. This suggests that the extended scenario provides a moderate improvement in network efficiency without substantially expanding the network.

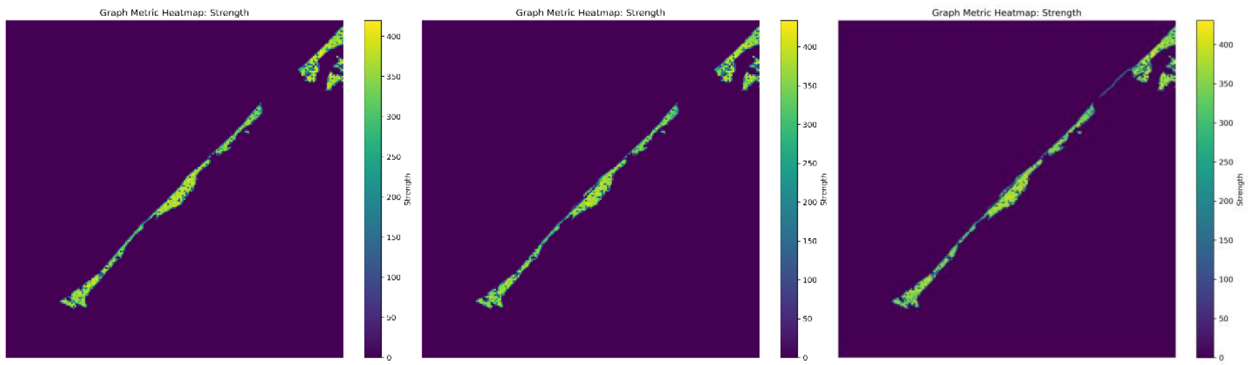


Figure 4.8. Local node strength across restoration scenarios for the Sandmotor (Delftlandse kust) site. *Maps show the no-demonstrator, baseline and extended restoration scenarios. Higher values indicate nodes that participate more strongly in successful dispersal connections.*

Overall, NL_Sandmotor shows a small but consistent connectivity response. The supporting metrics suggest that the site contributes positively through increased local cohesion and, under the extended scenario, modest improvements in movement efficiency.

4.9 NL_Texel

NL_Texel showed a small local demonstrator effect. IIC increased from 0.303 in the no-demonstrator scenario to 0.306 in the baseline scenario, corresponding to a relative gain of 1.0%. Clustering increased only slightly and density almost remains unchanged, while average path length and diameter also increased. This suggests a limited expansion effect rather than a major connecting effect. The extended scenario produced an equal small response, increasing IIC from 0.300 to 0.303, corresponding to a relative gain of 1.0%. Again, clustering increased slightly and density remains almost unchanged, while path length and diameter increased. This indicates incremental expansion of an already relatively connected network rather than a major improvement in movement efficiency.

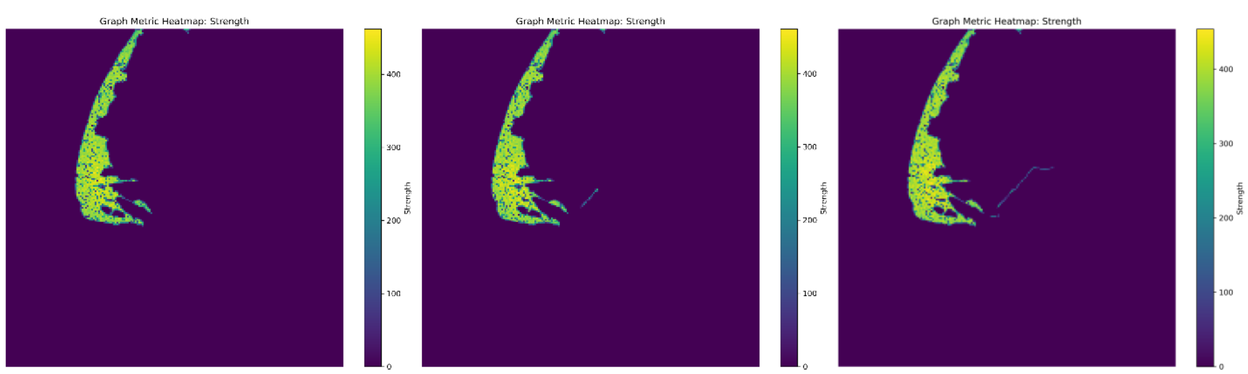


Figure 4.9. Local node strength across restoration scenarios for the Texel Prins Jan-Hendrikzanddijk site. *Maps show the no-demonstrator, baseline and extended restoration scenarios. Higher values indicate nodes that participate more strongly in successful dispersal connections.*

Overall, NL_Texel appears to be relatively well connected initially, with demonstrator and extended effects producing incremental rather than transformative gains. The supporting metrics suggest that both scenarios mainly extend or modestly strengthen the existing network.

4.10 PT_Porto

PT_Porto showed the strongest local demonstrator effect among all analysed sites. IIC increased from 0.133 in the no-demonstrator scenario to 0.164 in the baseline scenario, corresponding to a relative gain of 23.4%. This strong IIC response was accompanied by increases in density and clustering, and by strong decreases in average shortest path length and diameter. This combination indicates a clear connecting effect: the existing demonstrator substantially improves network efficiency and reduces fragmentation. The extended scenario also produced the strongest proportional response, increasing IIC from 0.066 to 0.132, corresponding to a relative gain of 100.0%. In the extended comparison, density and clustering increased strongly, but path length and diameter also increased, indicating that the extended scenario expands the spatial extent of the network while increasing link density.

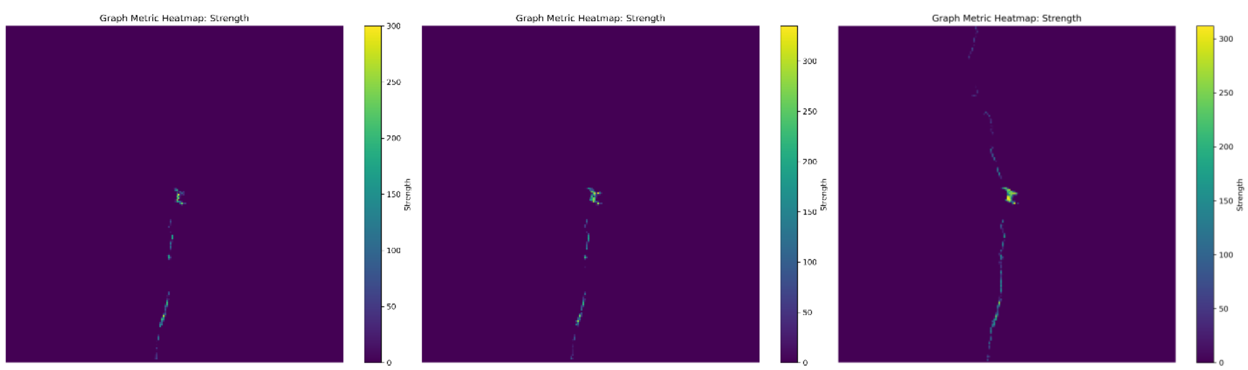


Figure 4.10. Local node strength across restoration scenarios for the Porto Sandpitch site. *Maps show the no-demonstrator, baseline and extended restoration scenarios. Higher values indicate nodes that participate more strongly in successful dispersal connections.*

Overall, PT_Porto stands out as one of the clearest examples of how dune-front restoration can improve regional connectivity.

4.11 SE_Ystad

SE_Ystad showed a small decrease in IIC with a decreased from 0.0193 in the no-demonstrator scenario to 0.0190 in the baseline scenario, corresponding to a relative gain of -1.4%. Absolute IIC values remained very low, indicating that SE_Ystad was among the least connected sites in the analysis. This is also reflected in the low node-strength values shown in Figure 4.11. Density remained constant and clustering increased strongly in relative terms, although this partly reflects very low initial clustering values. Average shortest path length and diameter also increased, suggesting that the local demonstrator adds habitat or local cohesion but does not overcome regional isolation. The extended scenario produced a much larger proportional response, increasing IIC from 0.009 to 0.017, corresponding to a relative gain of 83.8%. This was accompanied by strong increases in density and clustering, but also by large increases in average shortest path length and diameter. The extended scenario therefore expands and strengthens the network, but final absolute connectivity remains low.

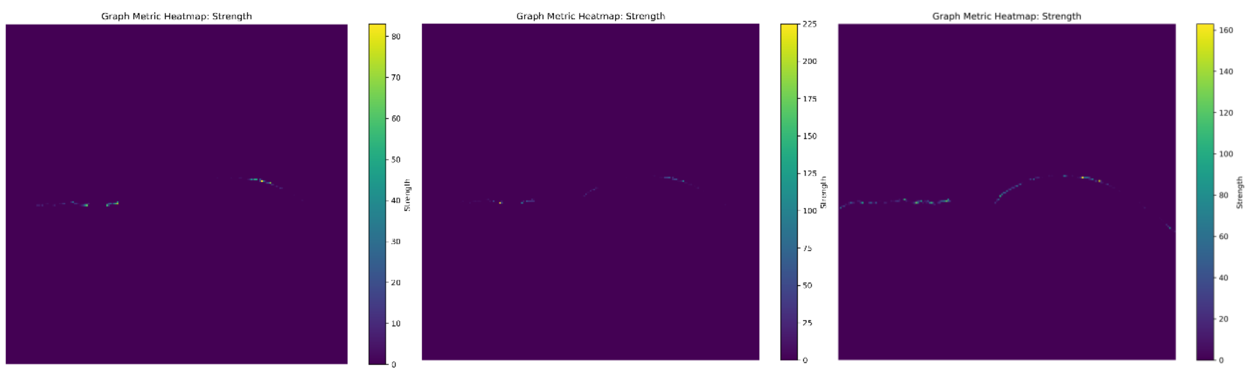


Figure 4.11. Local node strength across restoration scenarios for the Ystad site. *Maps show the no-demonstrator, baseline and extended restoration scenarios. Higher values indicate nodes that participate more strongly in successful dispersal connections.*

Overall, SE_Ystad represents a case of low absolute connectivity but high relative sensitivity to restoration. The supporting metrics suggest that restoration expands and locally strengthens the network but does not fully overcome regional isolation.

5. General discussion

5.1 General effects of dune-dike hybrid systems on ecological connectivity

The simulations show that dune-in-front-of-dike and other dune–dike hybrid interventions can contribute to regional ecological connectivity. Across the analysed demonstrators, the current baseline configurations generally increased IIC relative to the no-demonstrator scenarios, indicating that these interventions can provide biodiversity benefits beyond local habitat creation. By adding suitable dune habitat in otherwise fragmented coastal landscapes, demonstrators can function as stepping stones or local mobility nodes within broader alongshore networks.

The strength of this effect, however, varied substantially among sites. Some demonstrators produced clear gains in regional connectivity, whereas others had more limited effects under their current configuration and even decreased IIC. This variation indicates that the ecological performance of dune-front hybrids depends not only on the amount of habitat created, but also on where that habitat is located. Interventions positioned between existing dune patches, or within otherwise fragmented urban coastlines, are more likely to strengthen regional connectivity than interventions embedded in already well-connected networks or placed outside key movement bottlenecks.

The supporting network metrics further show that connectivity gains can arise through different mechanisms. In some cases, demonstrators improved network efficiency by shortening movement pathways between habitat cells. In others, IIC increased because the intervention expanded the spatial extent of the connected network, even when average path length or diameter also increased. This distinction is important for interpreting hybrid dune systems: longer network paths do not necessarily indicate poorer connectivity if they reflect the integration of additional habitat into a broader alongshore network.

Overall, the results support the use of dune-dike hybrid systems as connectivity-enhancing Nature-based Solutions but also show that their ecological value is strongly context-dependent. The most effective interventions are not simply those that create the most habitat, but those that add habitat in locations where it improves the structure and functioning of the wider coastal network.

5.2 Baseline connectivity and realised demonstrator performance

The baseline scenario represents the current demonstrator configuration and therefore provides an estimate of the connectivity already realised within each regional network. Sites with relatively high baseline IIC appear either to be embedded in better-connected coastal landscapes or to have demonstrator configurations that already capture much of the available connectivity benefit. In such cases, additional restoration may generate only limited gains unless it adds habitat in locations that alter the wider network structure.

This pattern was especially evident for several Dutch demonstrators. NL_HondsbosscheDuinen showed a strong realised demonstrator effect, but no additional gain under the extended scenario because the extended and baseline representations were identical in the available model output (i.e. the baseline coastline is already entirely lined with some form of dunes). NL_Katwijk, NL_Texel, and NL_Sandmotor also showed limited additional gains. These results suggest that larger or more established dune-front systems may already have realised a substantial part of their connectivity potential under the current configuration, at least within the spatial scenarios evaluated here.

By contrast, some sites with modest realised effects under the current configuration showed much stronger responses under extended restoration. FR_Dunkerque, for example, had relatively small local demonstrator effects but large extended-scenario gains. In the sites BE_combined, FR_Soulac, and SE_Ystad, we even observed a negative demonstrator effect on IIC. At the same time, average shortest path length and network diameter increased, while density and clustering showed small increases. This suggests that the present demonstrator footprint at these sites may be too limited, or too locally positioned, to strongly reorganise regional connectivity. A more extensive restoration configuration could therefore have a much larger effect if it adds habitat in locations that bridge existing network gaps.

Overall, baseline connectivity provides useful context for interpreting demonstrator performance. High baseline IIC may indicate that a site is already well integrated, whereas low or moderate baseline IIC can point to remaining opportunities for strategic restoration. The key distinction is whether additional habitat merely enlarges an existing network or whether it changes the way habitat patches are connected across the coastal landscape.

5.3 Potential for extending dune-front restoration

The extended restoration scenarios show that scaling up dune-front interventions can generate substantial additional connectivity benefits, especially in fragmented coastal networks. The largest gains occurred where added dune habitat was able to close spatial gaps, reinforce weak links or extend the network into poorly connected parts of the coast. This indicates that restoration potential is not determined by habitat area alone, but by the position of new habitat relative to the existing regional network.

The supporting metrics suggest that extended restoration can improve connectivity through two complementary mechanisms. In some sites, added habitat increased IIC while also reducing path length or diameter, indicating more efficient movement between habitat cells. In others, IIC increased together with path length or diameter, reflecting expansion of the connected network across a larger spatial extent. Both outcomes can be ecologically beneficial, but they imply different restoration effects: one improves movement efficiency within an existing network, whereas the other enlarges the spatial reach of connected habitat.

These differences have direct implications for planning. Where the objective is to reconnect fragmented dune patches, restoration should prioritise locations that act as stepping stones or close gaps between existing habitat clusters. Where networks are already relatively cohesive, additional habitat may mainly expand the available habitat base rather than fundamentally alter connectivity. In such cases, ecological gains may depend more on habitat quality, successional diversity and management than on further spatial expansion alone.

Overall, the extended scenarios show that dune-front restoration has the greatest potential when it changes the configuration of the coastal habitat network. Strategic placement is therefore critical: adding habitat in the right location can produce larger connectivity gains than simply increasing dune area where the network is already well connected.

5.4 Where is the greatest potential for improvement?

The greatest proportional potential for connectivity improvement occurred in sites with low initial connectivity. This pattern was clearest for the extended restoration scenarios, where initial IIC was strongly negatively related to relative IIC gain. In fragmented networks, even moderate additions of strategically placed dune habitat can produce large proportional improvements by closing gaps or creating new stepping-stone connections.

This finding suggests that dune-front restoration may be especially valuable along fragmented urban coastlines, where suitable dune habitat is sparse, discontinuous or interrupted by hard infrastructure. In such settings, new dune habitat can improve regional connectivity not only by increasing habitat area, but by changing how existing habitat patches are linked within the wider network.

However, high relative gain should not be interpreted as high restoration success on its own. Sites with very low initial IIC can show large proportional responses while remaining poorly connected in absolute terms. SE_Ystad illustrates this point: the extended scenario produced a large relative increase, but final IIC remained low compared with most other sites. Restoration therefore improved the network proportionally but did not fully overcome regional isolation.

The strongest candidates for additional restoration are those that combine large relative gains with meaningful absolute increases in IIC. PT_Porto, FR_SteMarie, FR_Dunkerque, DE_StPeterOrding and FR_Soulac stand out in this respect. In these sites, additional dune-front restoration appears capable of altering regional network structure, rather than merely enlarging an already connected habitat system.

5.5 Have larger or more mature demonstrators already realised their potential?

Some larger or more established demonstrators may already have realised much of their connectivity potential under the current configuration. This was particularly apparent for several Dutch sites. NL_HondsbosscheDuinen showed a strong local demonstrator effect but no additional improvement under the extended scenario, while NL_Katwijk and NL_Texel showed only limited additional gains. NL_Sandmotor showed a more moderate but consistent response. Together, these patterns suggest that the existing configurations already contribute substantially to regional connectivity, or that the tested extensions did not add habitat in locations that would substantially alter network structure.

In such systems, further biodiversity gains may depend less on adding more dune area and more on improving the ecological quality of the connected habitat. Connectivity is only meaningful if connected habitat can support colonisation, reproduction and persistence. Management priorities may therefore shift towards improving habitat quality, successional diversity, microhabitat heterogeneity, sand dynamics and disturbance regimes, rather than focusing primarily on further spatial expansion.

By contrast, sites with modest current demonstrator effects but large extended-scenario gains still appear to have unrealised structural potential. In these cases, spatial planning should identify where additional dune habitat would most effectively bridge network gaps, connect isolated habitat clusters or strengthen weak links in the regional coastal network.

5.6 Positive and negative implications of hybrid dune-front systems

The main positive implication is that dune-dike hybrid systems can contribute simultaneously to coastal protection and ecological network restoration. By placing dune habitat in front of dikes or urban infrastructure, these interventions can soften hard coastlines and create habitat elements that support alongshore connectivity. The modelling results show that, in several sites, these added habitat elements increased regional IIC, link density and local network cohesion.

At the same time, hybrid systems have clear limitations. Not every demonstrator strongly improved regional connectivity; some interventions mainly added local habitat without substantially changing the wider network. In addition, none of the simulated networks became strongly connected, indicating that dune-front restoration can reduce fragmentation but is unlikely to eliminate it entirely at the regional scale. These systems should therefore be viewed as contributions to broader ecological networks, rather than as stand-alone solutions for restoring full landscape connectivity.

A further limitation is that connectivity only translates into biodiversity benefits when the connected habitat is ecologically suitable. A dune strip that is well positioned in the network but poor in habitat quality may function less effectively than predicted by connectivity metrics alone. Habitat development, vegetation succession, sand dynamics and disturbance management are therefore essential components of connectivity restoration. This is particularly relevant for species or life stages that require minimum habitat area for reproduction, or that are sensitive to recreational pressure. The connectivity gains modelled here should therefore be interpreted as potential gains, conditional on the development and maintenance of suitable habitat conditions.

5.7 Habitat-quality assumptions and links with D5.1

A key assumption of the connectivity simulations is that habitat nodes are suitable according to the modelled habitat representation. The simulations therefore estimate potential functional connectivity, but they do not fully capture differences in habitat quality, successional stage or ecological maturity among demonstrators. This is important because D5.1 showed that habitat development varies among sites, including differences in the development of embryonic dunes, white dunes and grey dunes.

Mapped dune habitat may therefore differ in its actual suitability for the modelled arthropod-inspired communities. Newly created or restored dunes can vary in vegetation structure, sand dynamics, disturbance regime, microclimate, plant species composition and resource availability. These factors influence whether connected habitat patches can support colonisation, reproduction and persistence.

The integration of D5.1 and D5.3 is therefore essential. D5.1 describes habitat evolution and habitat-type development, whereas D5.3 evaluates whether those habitats are functionally connected within regional networks. A demonstrator with high connectivity potential but limited habitat quality may require management to improve ecological suitability. Conversely, a site with high-quality habitat but poor connectivity may benefit more from spatial expansion or stepping-stone creation. The strongest biodiversity outcomes are expected where habitat quality and functional connectivity develop together.

5.8 Implications for design and management

The results point to several design principles for future dune–dike hybrid systems. First, restoration should not focus only on increasing dune area. The spatial position of new habitat relative to existing dune patches is critical, because strategically placed habitat can generate large connectivity gains, especially in fragmented coastal networks. Second, sites with low initial connectivity may offer high proportional restoration potential, but final absolute connectivity should also be considered when setting priorities. Third, in already well-connected or spatially extensive demonstrator systems, further biodiversity gains may depend more on habitat quality, successional diversity and ecological management than on adding more dune area.

From a management perspective, dune-dike hybrids should be treated as dynamic ecological systems rather than static infrastructure elements. Their biodiversity value depends on both spatial configuration and habitat development through time. Management should therefore support the processes that make connected habitat ecologically functional, including vegetation development, sand dynamics, microhabitat heterogeneity and control of excessive disturbance where needed.

Future monitoring should combine remote-sensing-based habitat mapping, field-based biodiversity surveys and repeated connectivity modelling. This would make it possible to test whether the potential connectivity gains predicted here are realised as habitats mature and communities colonise restored dune systems. Such an integrated approach would also help identify whether management should prioritise additional habitat creation, improved habitat quality or better placement of future restoration measures.

6. References

Scientific literature

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs, 81*(2), 169–193. https://doi.org/10.1890/10-1510.1

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T. G., Chaput-Bardy, A., Clobert, J., Dytham, C., … Travis, J. M. J. (2012). Costs of dispersal. *Biological Reviews, 87*(2), 290–312. https://doi.org/10.1111/j.1469-185X.2011.00201.x

Brown, J. H., & Kodric-Brown, A. (1977). Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology, 58*(2), 445–449. https://doi.org/10.2307/1935620

Calabrese, J. M., & Fagan, W. F. (2004). A comparison-shopper's guide to connectivity metrics. *Frontiers in Ecology and the Environment, 2*(10), 529–536. https://doi.org/10.1890/1540-9295(2004)002[0529:ACGTCM]2.0.CO;2

Cardoso, P., Erwin, T. L., Borges, P. A. V., & New, T. R. (2011). The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation, 144*(11), 2647–2655. https://doi.org/10.1016/j.biocon.2011.07.024

Cheptou, P.-O., Hargreaves, A. L., Bonte, D., & Jacquemyn, H. (2017). Adaptation to fragmentation: Evolutionary dynamics driven by human influences. *Philosophical Transactions of the Royal Society B: Biological Sciences, 372*, 20160037. https://doi.org/10.1098/rstb.2016.0037

Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S., & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters, 12*(3), 197–209. https://doi.org/10.1111/j.1461-0248.2008.01267.x

Coleman, T. F., & Moré, J. J. (1983). Estimation of Sparse Jacobian Matrices and Graph Coloring Problems. SIAM Journal on Numerical Analysis, 20(1), 187–209.

DeAngelis, D. L., & Grimm, V. (2014). Individual-based models in ecology after four decades. *F1000Prime Reports, 6*, 39. https://doi.org/10.12703/P6-39

Foltête, J.-C. (2019). How ecological networks could benefit from landscape graphs: A response to the paper by Spartaco Gippoliti and Corrado Battisti. *Land Use Policy, 80*, 391–394. https://doi.org/10.1016/j.landusepol.2018.04.020

Galpern, P., Manseau, M., & Fall, A. (2011). Patch-based graphs of landscape connectivity: A guide to construction, analysis and application for conservation. *Biological Conservation, 144*(1), 44–55. https://doi.org/10.1016/j.biocon.2010.09.002

García, C., & Borda-de-Água, L. (2017). Extended dispersal kernels in a changing world: Insights from statistics of extremes. *Journal of Ecology, 105*(1), 63–74. https://doi.org/10.1111/1365-2745.12685

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances, 1*(2), e1500052. https://doi.org/10.1126/sciadv.1500052

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS ONE, 12*(10), e0185809. https://doi.org/10.1371/journal.pone.0185809

Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos* 87:209-219.

Hijmans R (2026). terra: Spatial Data Analysis. doi:10.32614/CRAN.package.terra

Hovestadt, T., Kubisch, A., & Poethke, H.-J. (2010). Information processing in models for density-dependent emigration: A comparison. *Ecological Modelling, 221*(3), 405–410. https://doi.org/10.1016/j.ecolmodel.2009.11.005

Keeley, A. T. H., Beier, P., & Jenness, J. S. (2021). Connectivity metrics for conservation planning and monitoring. *Biological Conservation, 255*, 109008. https://doi.org/10.1016/j.biocon.2021.109008

Lande, R., Engen, S., & Sæther, B.-E. (1998). Extinction times in finite metapopulation models with stochastic local dynamics. *Oikos, 83*(2), 383–389. https://doi.org/10.2307/3546853

Logghe, G., Batsleer, F., Maes, D., Permentier, T., Berg, M. P., Brosens, D., Cooleman, S., De Smedt, P., Hagge, J., Lambrechts, J., Pollet, M., Verheyde, F., & Bonte, D. (2025a). An in-depth dataset of northwestern European arthropod life histories and ecological traits. *Biodiversity Data Journal, 13*, e146785. https://doi.org/10.3897/BDJ.13.e146785

Logghe, G., Batsleer, F., Fandos, G., Maes, D., & Bonte, D. (2025b). Consistent covariation of dispersal, life history and thermal niches across terrestrial arthropods. *bioRxiv*. https://doi.org/10.1101/2025.01.10.632369

McLachlan, A., Defeo, O., & Hesp, P. A. (2025). Tandem ecosystems: A new perspective on ecological connectivity across the dune-beach interface on sandy shores. Estuarine, Coastal and Shelf Science, 326, 109530. https://doi.org/10.1016/j.ecss.2025.109530

Meurant, M., Gonzalez, A., Doxa, A., & Albert, C. H. (2018). Selecting surrogate species for connectivity conservation. *Biological Conservation, 227*, 326–334. https://doi.org/10.1016/j.biocon.2018.09.028

Mimet, A., Clauzel, C., & Foltête, J.-C. (2016). Locating wildlife crossings for multispecies connectivity across linear infrastructures. *Landscape Ecology, 31*, 1955–1973. https://doi.org/10.1007/s10980-016-0373-y

Minor, E. S., & Urban, D. L. (2008). A graph-theory framework for evaluating landscape connectivity and conservation planning. *Conservation Biology, 22*(2), 297–307. https://doi.org/10.1111/j.1523-1739.2007.00871.x

Mordacq, O. & Dahirel, M. (2025). DuneFront: Deliverable D5.1 - Habitat & vegetation evolution in Demonstrators. UGent: Gent. 61 pp. https://www.vliz.be/nl/imis?module=ref&refid=418887

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., ... Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature, 520*, 45–50. https://doi.org/10.1038/nature14324

Newman, M. E. J. (2003). Mixing patterns in networks. Physical Review E, 67(2), 026126. https://doi.org/10.1103/PhysRevE.67.026126

Pascual-Hortal, L., & Saura, S. (2006). Comparison and development of new graph-based landscape connectivity indices: Towards the priorization of habitat patches and corridors for conservation. *Landscape Ecology, 21*, 959–967. https://doi.org/10.1007/s10980-006-0013-z

Pascual-Hortal, L., & Saura, S. (2008). Integrating landscape connectivity in broad-scale forest planning through a new graph-based habitat availability methodology: Application to capercaillie (*Tetrao urogallus*) in Catalonia, NE Spain. *European Journal of Forest Research, 127*, 23–31. https://doi.org/10.1007/s10342-006-0165-z

Pebesma, E., 2018. Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal 10 (1), 439-446, https://doi.org/10.32614/RJ-2018-009

Prima, M.-C., Renaud, J., Witté, I., Suarez, L., Rouveyrol, P., Fernando, M., Sacchi, A., Cosentino, F., Santini, L., Maiorano, L., Moreira, F., Dertien, J., Fernández, N., & Thuiller, W. (2024). A comprehensive framework to assess multi-species landscape connectivity. *Methods in Ecology and Evolution, 15*(12), 2385–2399. https://doi.org/10.1111/2041-210X.14444

R Core Team (2025). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Robin, N., Ruz, M.-H., Castelle, B. & Blaise, E. (2024). DuneFront: Deliverable 6.1 - Morphodynamics patterns. 69 pp. https://www.vliz.be/en/imis?module=ref&refid=409899

Sahraoui, Y., Foltête, J.-C., & Clauzel, C. (2017). A multi-species approach for assessing the impact of land-cover changes on landscape connectivity. *Landscape Ecology, 32*, 1819–1835. https://doi.org/10.1007/s10980-017-0551-6

Sánchez-Bayo, F., & Wyckhuys, K. A. G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation, 232*, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020

Santini, L., Cornulier, T., Bullock, J. M., Palmer, S. C. F., White, S. M., Hodgson, J. A., Bocedi, G., & Travis, J. M. J. (2016). A trait-based approach for predicting species responses to environmental change from sparse data: How well might terrestrial mammals track climate change? *Global Change Biology, 22*(7), 2415–2424. https://doi.org/10.1111/gcb.13271

Saura, S., Bodin, Ö., & Fortin, M.-J. (2014). Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology, 51*(1), 171–182. https://doi.org/10.1111/1365-2664.12179

Saura, S., & Pascual-Hortal, L. (2007). A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. *Landscape and Urban Planning, 83*(2–3), 91–103. https://doi.org/10.1016/j.landurbplan.2007.03.005

Templeton, A. R., Shaw, K., Routman, E., & Davis, S. K. (1990). The genetic consequences of habitat fragmentation. *Annals of the Missouri Botanical Garden, 77*(1), 13–27. https://doi.org/10.2307/2399621

Travis, J. M. J., Mustin, K., Barton, K. A., Benton, T. G., Clobert, J., Delgado, M. M., Dytham, C., Hovestadt, T., Palmer, S. C. F., Van Dyck, H., & Bonte, D. (2012). Modelling dispersal: An eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. *Methods in Ecology and Evolution, 3*(4), 628–641. https://doi.org/10.1111/j.2041-210X.2012.00193.x

Urban, D., & Keitt, T. (2001). Landscape connectivity: A graph-theoretic perspective. *Ecology, 82*(5), 1205–1218. https://doi.org/10.1890/0012-9658(2001)082[1205:LCAGTP]2.0.CO;2

Van De Walle, R., Dahirel, M., Langeraert, W. *et al*. Drivers of plant-associated invertebrate community structure in West-European coastal dunes. *npj biodivers* **4**, 12 (2025). https://doi.org/10.1038/s44185-025-00084-8

Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., & Stopak, D. (2021). Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences, 118*(2), e2023989118. https://doi.org/10.1073/pnas.2023989118

Watts, D. J., & Strogatz, S. H. (1998). Collective dynamics of 'small-world' networks. Nature, 393(6684), 440–442. https://doi.org/10.1038/30918

Wood, S. L. R., Martins, K. T., Dumais-Lalonde, V., Tanguy, O., Maure, F., St-Denis, A., Rayfield, B., Martin, A. E., & Gonzalez, A. (2022). Missing interactions: The current state of multispecies connectivity analysis. *Frontiers in Ecology and Evolution, 10*, 830822. https://doi.org/10.3389/fevo.2022.830822

Policy, legal and institutional references

Copernicus Land Monitoring Service (2021). Coastal Zones Land Cover/Land Use 2018 (vector), Europe, 6-yearly. https://doi.org/10.2909/205e2db2-4e35-4b1b-bf84-271c4a82248c

Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Communities, L 206*, 7–50. http://data.europa.eu/eli/dir/1992/43/2025-07-14

Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds. *Official Journal of the European Union, L 20*, 7–25. http://data.europa.eu/eli/dir/2009/147/2019-06-26

European Commission. (2013). *Green Infrastructure (GI): Enhancing Europe's natural capital* (COM(2013) 249 final). https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:52013DC0249

European Commission. (2020). *EU Biodiversity Strategy for 2030: Bringing nature back into our lives* (COM(2020) 380 final). https://environment.ec.europa.eu/strategy/biodiversity-strategy-2030_en

European Commission. (n.d.). *Green infrastructure*. https://environment.ec.europa.eu/topics/nature-and-biodiversity/green-infrastructure_en

IPBES. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. IPBES Secretariat. https://doi.org/10.5281/zenodo.3553579

Regulation (EU) 2024/1991 of the European Parliament and of the Council of 24 June 2024 on nature restoration and amending Regulation (EU) 2022/869. *Official Journal of the European Union, L 2024/1991*. http://data.europa.eu/eli/reg/2024/1991/oj

7. Appendices

Appendix 2.5 Regional connectivity metrics

Regional ecological connectivity was quantified from the scenario-specific dispersal networks constructed for each demonstrator. In these networks, habitat cells were represented as nodes, considering the map in the comparison with the most habitat cells, and successful dispersal events as functional links. This graph-based approach follows the landscape-graph tradition in connectivity ecology, where habitat elements are treated as nodes and movement or dispersal connections as edges.

All regional metrics were calculated on the unweighted network meaning edge weight was not considered. The metric selection was designed to capture complementary aspects of regional connectivity. The Integral Index of Connectivity was used as the main synthetic indicator because it combines habitat availability with network reachability (Keeley et al., 2021; Pascual-Hortal & Saura, 2006). Additional graph metrics- including strong connectivity indicator, average shortest path length, network diameter, global clustering coefficient, network density, degree and attribute assortativity - were used to interpret the structural mechanisms underlying changes in connectivity among scenarios (Coleman & Moré, 1983; Minor & Urban, 2008; Newman, 2003; Watts & Strogatz, 1998).

Integral Index of Connectivity

The **Integral Index of Connectivity** (IIC) was used as the primary indicator of regional ecological connectivity. IIC is a graph-based habitat-availability metric that accounts for both the amount of habitat in a landscape and the degree to which habitat nodes are connected through the network (Keeley et al., 2021; Pascual-Hortal & Saura, 2006). It is therefore more informative than habitat area alone, because it incorporates the spatial arrangement of habitat and the existence of movement pathways among habitat elements.

To calculate the IIC values the carrying capacity of the nodes were used. As described above the carrying capacity assigned to a node depends on the maps being compared. For this reason, the baseline map from one site has different IIC values depending on the comparison scenario. However, since the other regional metrics, besides attribute assortativity, do not use carrying capacity in their calculations, and the three maps within a site do not otherwise differ in habitat cells, the other regional metrics remain constant per map, independent of the comparison scenario. (The number of habitat cells, cells with a carrying capacity greater than or equal to zero, in the different maps of one site remain constant since habitat cells present in one map but absent in another are assigned a carrying capacity of zero in the latter map.)

In D5.3, higher IIC values indicate stronger functional integration of suitable dune habitat within the regional network. Increases in IIC between scenarios were interpreted as improved potential for dispersal, recolonisation and metacommunity persistence. Lower IIC values indicate a more fragmented network, in which suitable habitat cells are more isolated or connected through less efficient movement pathways.

IIC was used as the main measure of restoration performance because DuneFront demonstrators may contribute to biodiversity both by creating habitat and by acting as stepping stones between existing dune patches. Scenario-specific IIC values were therefore used to compare the realised contribution of existing demonstrators and the additional connectivity gain associated with extended restoration.

Network density, clustering and path-based metrics

Several supporting network metrics were used to interpret how connectivity changed between scenarios.

Network density describes the proportion of possible links between nodes that are realised in the simulated network (Coleman & Moré, 1983). Higher density indicates that a larger fraction of potential source–destination connections is functionally realised. Ecologically, this may reflect a more redundant movement network with more alternative dispersal routes. Density was interpreted cautiously when the number of nodes differed among scenarios, because adding habitat cells changes both the number of possible links and the number of realised links.

The **global clustering coefficient** measures the tendency of connected nodes to form locally cohesive groups (Watts & Strogatz, 1998). Higher clustering indicates that habitat cells are embedded in neighbourhoods where several nodes are mutually connected. This can reflect stronger local stepping-stone structure, greater local cohesion and more redundancy in short-distance dispersal routes (Minor & Urban, 2008). Since the function used to calculate this metric does not yet support directed graphs, it was calculated on the undirected graph.

Two path-based metrics were used: average shortest path length and diameter. **Average shortest path length** is the mean number of network steps required to connect pairs of reachable nodes (Watts & Strogatz, 1998). Lower values generally indicate more efficient movement through the network. **Diameter** is the longest shortest path within the connected part of the network and describes the maximum network distance across the system (Urban

& Keitt, 2001). The network diameter is indicative of speed of movement through a network; i.e. short diameter implies fast movement through the network (Minor & Urban, 2008).

Path-based metrics were interpreted in relation to IIC and network size. In restoration scenarios, additional habitat can make a network larger and more spatially extensive. In such cases, average shortest path length or diameter may increase even when overall connectivity improves. Therefore, increases in path length or diameter were not automatically interpreted as negative; they were evaluated together with IIC, density and clustering.

The **strong connectivity indicator** was used to assess whether all nodes were mutually reachable in the directed network. A strongly connected network implies that every node can be reached from every other node through directed links. In this analysis, the metric served as a high-level indicator of complete regional integration.

Assortativity metrics

Assortativity metrics were used to describe how links are organised with respect to node properties. Unlike IIC, density or clustering, assortativity does not provide a simple measure of better or worse connectivity. It describes network organisation.

Degree assortativity measures whether nodes tend to connect to other nodes with a similar number of links (Newman, 2003). Positive degree assortativity indicates that highly connected nodes tend to connect to other highly connected nodes, whereas negative values indicate a more hub–periphery structure, where highly connected nodes often link to less connected nodes. In ecological terms, increasing degree assortativity may reflect consolidation of a connected core, while decreasing assortativity may indicate new links between central and peripheral habitat cells.

Attribute assortativity measures whether nodes with similar attributes tend to be connected (Newman, 2003). The interpretation depends on the attribute used, such as habitat type, carrying capacity or another node-level characteristic. Positive attribute assortativity indicates stronger linkage among similar nodes, whereas lower or negative values indicate more frequent links among dissimilar nodes. As the simulation used carrying capacity as the node attribute, the attribute assortativity values for the baseline map can differ depending on the tested scenario.

Assortativity metrics were therefore interpreted as descriptors of network organisation rather than as direct indicators of restoration success. Changes in assortativity were evaluated alongside IIC and the supporting structural metrics.

Appendix 3.3: Regional network statistics for each demonstrator site under the no-demonstrator, baseline demonstrator and extended restoration scenarios. IIC is excluded because it is reported separately as the main synthetic connectivity metric.

Site	Regional statistic	No demonstrator	Baseline (Local demonstrator effect)	Baseline (Extended scenario)	Extended scenario
BE_combined	network_strongly_connected	FALSE	FALSE	FALSE	FALSE
	average_shortest_path_length	4.4681	4.7370	4.7369	4.9810
	diameter	11	13	13	15
	global_clustering_coeff	0.1615	0.1629	0.1629	0.1723
	density	0.0136	0.0136	0.0136	0.0143
	degree_assortativity	0.5511	0.5387	0.5387	0.5597
	attribute_assortativity	0.0415	0.0417	0.0417	0.0490
DE_StPeterOrding	network_strongly_connected	FALSE	FALSE	FALSE	FALSE
	average_shortest_path_length	2.6687	2.5472	2.5472	2.7944
	diameter	7	6	6	7
	global_clustering_coeff	0.1240	0.1309	0.1309	0.1457
	density	0.0197	0.0228	0.0228	0.0261
	degree_assortativity	0.2532	0.2494	0.2494	0.3543
	attribute_assortativity	0.0525	0.0380	0.0380	0.0640
FR_Dunkerque	network_strongly_connected	FALSE	FALSE	FALSE	FALSE
	average_shortest_path_length	2.1482	2.1575	2.1575	3.9018
	diameter	4	4	4	13
	global_clustering_coeff	0.1565	0.1598	0.1598	0.1838
	density	0.0261	0.0263	0.0263	0.0299
	degree_assortativity	0.3164	0.3168	0.3168	0.4391
	attribute_assortativity	0.0344	0.0253	0.0253	0.0631
FR_Soulac	network_strongly_connected	FALSE	FALSE	FALSE	FALSE
	average_shortest_path_length	3.9743	4.3551	4.3551	4.0864
	diameter	10	12	12	11
	global_clustering_coeff	0.1363	0.1389	0.1389	0.1489
	density	0.0141	0.0145	0.0145	0.0169
	degree_assortativity	0.2176	0.2217	0.2217	0.2516
	attribute_assortativity	0.1067	0.0933	0.0930	0.1023
FR_SteMarie	network_strongly_connected	FALSE	FALSE	FALSE	FALSE
	average_shortest_path_length	3.3095	4.4687	4.4687	5.4189
	diameter	8	10	10	15
	global_clustering_coeff	0.1202	0.1238	0.1238	0.1528
	density	0.0144	0.0146	0.0146	0.0188
	degree_assortativity	0.3889	0.3972	0.3972	0.4417
	attribute_assortativity	0.0915	0.1024	0.1023	0.1089
NL_HondsbosscheDuinen	network_strongly_connected	FALSE	FALSE	FALSE	FALSE
	average_shortest_path_length	2.9822	2.9845	2.9845	2.9845
	diameter	6	6	6	6
	global_clustering_coeff	0.1865	0.1955	0.1955	0.1955
	density	0.0216	0.0224	0.0224	0.0224
	degree_assortativity	0.3507	0.3922	0.3922	0.3922
	attribute_assortativity	0.0440	0.0466	0.0466	0.0466
NL_Katwijk	network_strongly_connected	FALSE	FALSE	FALSE	FALSE
	average_shortest_path_length	3.014444	3.021555	3.021555	3.038353
	diameter	7	7	7	7
	global_clustering_coeff	0.1916	0.1911	0.1911	0.1939
	density	0.0182	0.0184	0.0184	0.0185

	degree_assortativity	0.4524	0.4542	0.4542	0.4533
	attribute_assortativity	0.0170	0.0190	0.0190	0.0194
NL_Sandmotor	network_strongly_connected	FALSE	FALSE	FALSE	FALSE
	average_shortest_path_length	3.2833	3.4035	3.4035	3.2981
	diameter	7	7	7	7
	global_clustering_coeff	0.2150	0.2234	0.2234	0.2226
	density	0.0223	0.0234	0.0234	0.0237
	degree_assortativity	0.2670	0.2522	0.2522	0.2640
	attribute_assortativity	0.0338	0.0280	0.0282	0.0318
NL_Texel	network_strongly_connected	FALSE	FALSE	FALSE	FALSE
	average_shortest_path_length	2.3620	2.3840	2.384	2.4197
	diameter	5	6	6	8
	global_clustering_coeff	0.1966	0.1983	0.1983	0.2016
	density	0.0372	0.0373	0.0373	0.0376
	degree_assortativity	0.3556	0.3576	0.3576	0.3741
	attribute_assortativity	0.0370	0.0424	0.0424	0.0488
PT_Porto	network_strongly_connected	FALSE	FALSE	FALSE	FALSE
	average_shortest_path_length	5.3720	2.7528	2.7528	4.4944
	diameter	12	6	6	12
	global_clustering_coeff	0.0602	0.0680	0.0680	0.0773
	density	0.0051	0.0069	0.0069	0.0115
	degree_assortativity	0.1832	0.3216	0.3216	0.4141
	attribute_assortativity	0.2474	0.1936	0.1901	0.2045
SE_Ystad	network_strongly_connected	FALSE	FALSE	FALSE	FALSE
	average_shortest_path_length	1.3333	1.7500	1.7500	4.3788
	diameter	2	3	3	10
	global_clustering_coeff	0.0067	0.0173	0.0173	0.0283
	density	0.0012	0.0012	0.0012	0.0034
	degree_assortativity	0.2136	0.2443	0.2443	0.2401
	attribute_assortativity	0.4667	0.4754	0.4759	0.4171