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Habitat functionality: Integrating environmental and geographic space in niche modeling for conservation planning

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Abstract

Niche modeling is typically used to assess the effects of anthropogenic land use and climate change on species distributions and to inform spatial conservation planning. These models focus on the suitability of local biotic and abiotic conditions for a species in environmental space (E-space). Although movements also affect species occurrence, efforts to formally integrate geographic space (G-space) into niche modeling have been hindered by the lack of comprehensive theoretical frameworks. We propose the "functional habitat" framework to define areas that are simultaneously of high quality in E-space, and functionally connected to other suitable habitats in G-space. Originating in metapopulation ecology, approaches have been developed to assess the amount of suitable connected habitats, based on the proximity between pairs of locations. Using network theory, which operates in topological space (T-space, defined by a network), we extended these metapopulation approaches to integrate movement constraints in G-space with niche modeling in E-space. We demonstrate the functional habitat framework using empirical data (GPS tracking and population monitoring) throughout the European wild mountain reindeer (*Rangifer t. tarandus*) distribution range. We show that functional habitat outperforms traditional suitability in explaining the species' distribution. This approach integrates effects from habitat loss and fragmentation for spatial conservation planning, and avoids overemphasizing small, inaccessible areas with locally suitable habitats. The functional habitat framework formally integrates biotic, abiotic, and movement constraints in niche modeling using network theory, thus opening a wide range of applications in spatial conservation planning.

KEYWORDS
connectivity, fragmentation, habitat, habitat loss, metapopulation theory, network theory, niche, *Rangifer*, species distribution

INTRODUCTION

The current loss of biodiversity globally is due to anthropogenic land use and climate change (Haddad et al., 2015; IPBES, 2019) that reduce species ranges and population sizes. Anthropogenic impacts on species ranges are commonly quantified using niche models, including species distribution models (Guisan & Zimmermann, 2000) and resource selection models (Boyce & McDonald, 1999; Manly et al., 2007). These models typically study factors driving species and population distribution by assessing the suitability of local environmental conditions in environmental space (i.e., focusing on environmental conditions required for the species' existence; see Guisan et al., 2017). A species' distribution is determined not only by the suitability of local biotic and abiotic conditions, but also by their accessibility through movements, as described in the biotic–abiotic–movement (BAM; Figure 1) framework (Soberon & Peterson, 2005). Although, movements are crucial determinants of species distributions, they remain unaccounted for in ~80% of studies (Holloway & Miller, 2017; Seaborn et al., 2020). This contributes to the mismatch often detected between the predictions of habitat suitability models and the observed species' distribution, which may be caused, for example, by the species' ab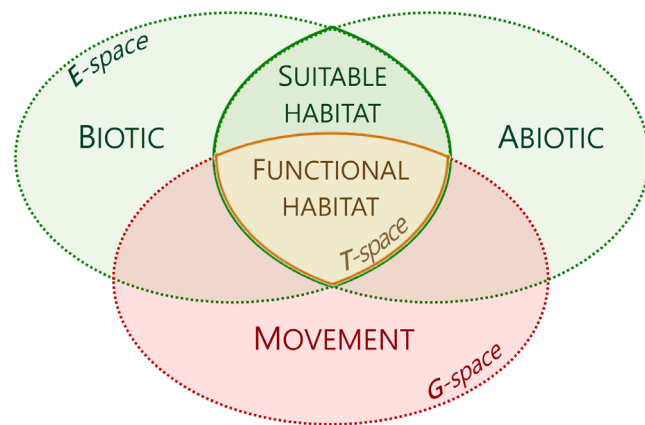sence from suitable habitat due to dispersal constraints (Matthiopoulos, 2022, and references therein). The main challenge to integrating movements in niche models is that while habitat suitability is assessed in environmental space (E-space), assessing its accessibility requires the simultaneous consideration of the spatial configuration of resources and barriers in geographic space (G-space, i.e., longitude–latitude–altitude) and topological space (T-space, i.e., the species-specific ecological connectivity between areas in a landscape network; Jordán & Scheuring, 2004). In this paper, we present a theoretical and methodological framework integrating network theory, metapopulation theory, and niche theory, to assess what we term "functional habitats," that is, suitable habitats that are functionally connected in the topological space of a landscape's spatial network.

Environmental niche models commonly focus on the local biotic and abiotic conditions that contribute to the occupancy of a location by a species (e.g., Guisan et al., 2017). Kearney (2006) defines habitat as "a description of the physical nature (biotic and abiotic) of a place of interest with respect to an organism," that is the location's position in E-space. Although habitat suitability is often predicted onto maps (G-space), the spatial relationships among mapping units, such as the distance or connectivity between pixels or cells of suitable habitat, are generally not taken into account (Matthiopoulos et al., 2020). Thus, high-resolution mapping risks identifying islets of "suitable" habitats that are too small and isolated, and therefore functionally unsuitable, to support an individual or a population. In other words, although an area may present suitable biotic and abiotic conditions in E-space, it may still be unsuitable from a G/T-space perspective if it is not connected to other suitable habitats (Figure 2).

In metapopulation theory, Hanski and Ovaskainen developed two metrics to integrate the amount and the connectedness of habitat in a landscape: the neighborhood habitat area index (NHAI; pp. 83 in Hanski, 1999) and the metapopulation capacity (MC; Hanski & Ovaskainen, 2000). Originally, both metrics were developed using a patch-matrix model of the landscape (reviewed in Lausch et al., 2015) with simple connectivity metrics based on the Euclidean distance between areas, ignoring landscape heterogeneity in between these areas. Subsequent research has addressed this major limitation using network-based ecological distances (i.e., least-cost distance or resistance distance) to account for the role of landscape heterogeneity for connectivity, as presented by, for instance, "stepping stones" (e.g., Drielsma, Manion, & Ferrier, 2007; Gurrutxaga et al., 2011; Saura & Pascual-Hortal, 2007). These metapopulation- and network-based approaches present an approach for incorporating spatial relationships into niche modeling, and

FIGURE 1 Contextualization of "functional habitat" in the biotic–abiotic–movement (BAM) niche framework (Soberon & Peterson, 2005). According to the BAM framework, the distribution of a species is determined by the biotic and abiotic niche (ABIOTIC [A] and BIOTIC [B], in green, both defined in environmental space, E-space), and by movement (MOVEMENT [M], in red, defined in geographic space, G-space). The geographic range with conditions at the intersection of the abiotic and biotic niche ($B \cap A$) is considered "suitable habitat," whereas the intersection of all three factors ($B \cap A \cap M$) represents the "functional habitat," that is, a subset of suitable habitat, that is simultaneously suitable and accessible. Functional habitat therefore integrates E-space and G-space, and it is defined in topological space (T-space).
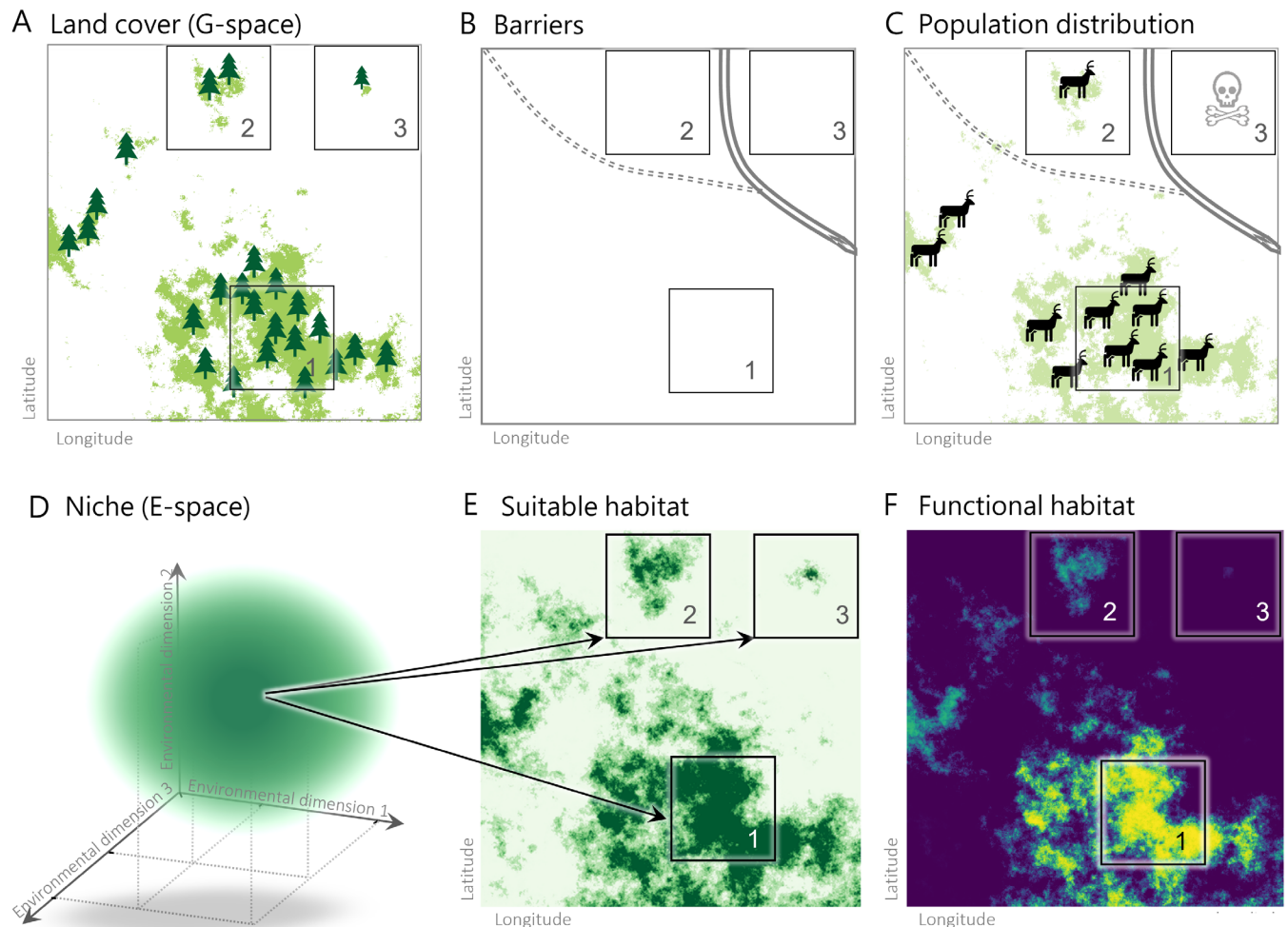
FIGURE 2 Conceptual framework of functional habitat. The upper row illustrates a landscape in geographic space, with forested areas (panel A) and roads (panel B), and highlights three areas within (1, 2, 3). A hypothetical deer species prefers forested habitat and can traverse small roads, while larger roads present nearly impermeable barriers. Thus (panel C), the highest abundance of individuals is expected in the largest and most continuous forested habitat (1), while no deer is expected to survive in the small and isolated habitat patch in (3). The bottom row illustrates different representations of the species' niche. The ecological niche can be represented in environmental space (panel D), and can be predicted in geographic space as a traditional habitat suitability map ignoring connectivity (panel E), or as a network-based map of functional habitat (panel F). While pixels of highly suitable habitat (darker green) are present in areas 1, 2, and 3, pixels of highly functional habitat (bright yellow) can be detected only in 1, and to a far lower degree in 2 with virtually no functional habitat in area 3. This is because functional habitat is a subset of suitable habitat, that is at the same time highly suitable and well connected. Thus, while within the three areas identical conditions in E-space are present, they do not represent the same potential for individual or population viability. In other words, the long-term persistence of individuals in an area is not solely determined by E-space, but also by G-space. See main text for further details.

allowing them to overcome the "nearsightedness" of traditional habitat suitability maps by including connectivity among areas. However, fully optimal or completely random movements represent two extremes on a continuum with animals often moving in between (Goicolea et al., 2021; Panzacchi et al., 2016).

In general, from a network perspective, the connectivity between two areas increases as the cost of moving along the paths between them decreases and as the number of alternative paths increases. The least-cost distance

and the resistance distance (based on an optimal and a random walker, respectively) each measure only one of these aspects, that is, the cost or the number of paths, respectively (Van Moorter et al., 2021). In contrast, the randomized shortest paths framework (RSP; Kivimäki et al., 2014; Saerens et al., 2009) uses a "randomness" parameter to interpolate between both extremes (fully optimal vs. fully random movements), thus accounting simultaneously for both the cost and the number of paths between two areas. This enhances the ability to tailor the

models to the specific species' movement patterns, and thus the accuracy and realism in the representation of connectivity (Panzacchi et al., 2016). Owing to its flexibility, the RSP framework is gaining popularity in movement ecology (e.g., Brennan et al., 2018; Fullman et al., 2017; Goicolea et al., 2021; Peck et al., 2017; Vasudev et al., 2021). Building on this framework, Van Moorter et al. (2021) defined and quantified "effective connectivity" between two locations, considering simultaneously their suitability and functional connectivity for a focal ecological process.

In this paper, we propose the "functional habitat" framework for niche modeling by formally integrating habitat suitability in E-space with its accessibility in G-space (Figure 1). In practice, we scale up the quantification of effective connectivity in Van Moorter et al. (2021) from a single pair of locations to an all-pairs approach, which allows us to quantify the effective connectivity at the landscape scale using the connectivity modeling library ConScape (Van Moorter, Kivimäki, Noack, et al., 2023; Figure 3). Effectively connected areas at the landscape scale represent "functional habitats," defined as areas that are simultaneously suitable and functionally connected to other suitable habitats. We first formally define functional habitat as an extension of current metapopulation theoretical approaches. We then empirically test the ability of the functional versus suitable habitat to explain the population distribution of wild mountain reindeer (*Rangifer t. tarandus*) throughout their distribution range in Norway, using both GPS tracking (Panzacchi et al., 2015) and population monitoring data (Nilsen & Strand, 2018).

METHODS

Functional habitat: Definition

Different metrics have been developed in metapopulation ecology to simultaneously quantify the effects of habitat loss and landscape fragmentation on populations (reviewed in Kindlmann & Burel, 2008; Saura & Pascual-Hortal, 2007).
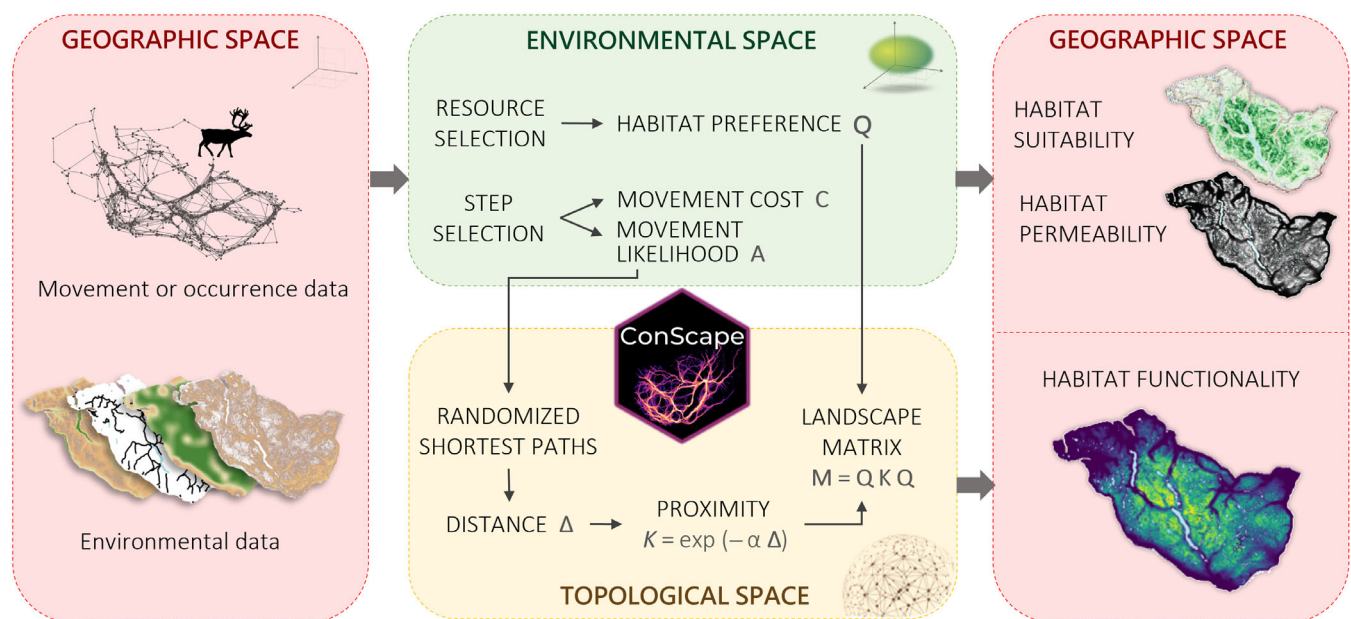

FIGURE 3　Analytical workflow to compute functional habitat. First, species' data and environmental variables (defined in geographic space, G-space) are modeled to obtain a representation of the species' niche in environmental space (E-space), describing both the suitability of resources for the species' occurrence, and their permeability to movements. These metrics are typically predicted back in the G-space. We used resource selection functions (RSF, Panzacchi et al., 2015) and step selection functions (SSF, Panzacchi et al., 2016), but other approaches (e.g., integrated step selection analysis; Avgar et al., 2016) can be used (see also Van Moorter et al., 2021, for a discussion of other data types). The software ConScape (Connected Landscapes; Van Moorter, Kivimäki, Noack, et al., 2023) then parameterizes a landscape network, or graph, in topological space (*T*), using habitat preferences as proxy for the quality $\mathbf{Q}$ of nodes, and the likelihood $\mathbf{A}$ and cost $\mathbf{C}$ of movements as attributes for the links (see Van Moorter et al., 2021). The Randomized Shortest Paths algorithm (Saerens et al., 2009) computes the ecological distance (Δ) between a pair of source and target pixels s and t, and their proximity ($\mathbf{K} = \exp(-\alpha\Delta)$). The "landscape matrix" $\mathbf{M}$ is computed by multiplying the habitat quality from E-space ($\mathbf{Q}$) with the proximity in T-space ($\mathbf{K}$) for each pixel pair $s - t$. This matrix can then be summarized using summation or eigenanalysis to estimate functional habitat in each pixel, which can be visualized in G-space (see main text for further details).

The formalism, based on the landscape matrix (**M**), for the two most common approaches was first presented by Hanski and Ovaskainen (Hanski, 1999; Hanski & Ovaskainen, 2000) as NHAI (pp. 83 in Hanski, 1999) and MC (Hanski & Ovaskainen, 2000). The matrix **M** consists of elements $m_{st} = q_s \times q_t \times \exp(-\alpha d_{st})$, where q is the quality and d_{st} is the distance between all pairs of areas as source s and target t, scaled with species-specific movement capabilities α. Note that we use the term "matrix" in its mathematical meaning, not as the area in between habitat patches (cf. the patch-matrix representation of a landscape; Lausch et al., 2015). The difference between NHAI and MC lies in the summary statistics derived from the landscape matrix **M**, respectively, the sum of its elements versus its leading eigenvalue. We present a brief overview of this foundational work and later developments (e.g., Drielsma, Ferrier, & Manion, 2007; Saura & Pascual-Hortal, 2007) in Appendix S1: Section S1.1.

We extended these metapopulation approaches through the concept of "functional habitat," which refers to habitats that are simultaneously suitable in environmental space and accessible in geographic space, or functionally connected in topological space to other suitable habitats (Figure 1). The term functional habitat was first used by Dennis et al. (2003) to denote the habitats "...where resources are connected by daily movements..." (Van Dyck, 2012, p. 149) or, in other words, habitats that are simultaneously suitable and well connected. Based on the BAM framework we generalize this definition by including larger scale movements. We formally defined functional habitat as a summary of the landscape matrix **M** with elements $m_{st} = q_s \times q_t \times k_{st}$, which quantifies (1) the suitability q of a landscape unit s or t in environmental space; and (2) the connectivity or proximity k_{st} between a pair of landscape units as source s and target t in geographic or topological space (Figure 3; note: $k_{st} = 1$ for $s = t$, thus allowing for self-rescue; Saura & Pascual-Hortal, 2007; Schnell et al., 2010).

We can then define the functional habitat $\mathcal{K}$ of a landscape (L), or in short, the landscape functionality, in two ways: first, by summing all the elements of the landscape matrix **M**:

$$\mathcal{K}^{\text{sum,L}} = \sum_{s=1}^{n} \sum_{t=1}^{n} m_{st} = \sum_{s=1}^{n} \sum_{t=1}^{n} q_s q_t k_{st}, \qquad (1)$$

and second, by the leading eigenvalue from **M**:

$$\mathcal{K}^{\text{eig,L}} = \lambda_1^{\downarrow}(\mathbf{M}). \qquad (2)$$

Whether the summary should emphasize connectivity recursively ($\mathcal{K}^{\text{eig,L}}$) or nonrecursively ($\mathcal{K}^{\text{sum,L}}$) will depend on the ecological application. For instance, metapopulation persistence may be better assessed recursively, whereas a nonrecursive approach may be better suited for migration connectivity. However, computational constraints may also affect this choice, as the summation of **M** is computationally less demanding than eigenanalysis and the absence of recursive connectivity makes the implementation of moving window approaches more straightforward for summation-based functional habitat. For these computational reasons, we focused our current presentation and demonstration on summation-based functional habitats. See Appendix S1: Section S1.2 for details and the discussion of functional habitat based on eigenanalysis.

In addition to summarizing the whole landscape, we can also define functional habitat for each landscape unit s or t in an analogous manner: first, by summing over all columns of **M**:

$$\mathcal{K}_s^{\text{sum,s}} = \sum_{t=1}^{n} q_s q_t k_{st}, \qquad (3)$$

this metric quantifies how well high-quality source pixels are connected to suitable target habitat within a landscape. Alternatively, summing over all rows of **M**:

$$\mathcal{K}_t^{\text{sum,t}} = \sum_{s=1}^{n} q_s q_t k_{st}, \qquad (4)$$

quantifies the functionality of target pixels t, that is, how well suitable targets are connected to suitable source habitats.

Initially, in Hanski's work, the proximity between the source and target (k_{st}) was an exponential decay function of the Euclidean distance (d_{st}^{Eucl}): $k_{st} = \exp(-\alpha d_{st}^{\text{Eucl}})$ (with distance scaling parameter α; Hanski, 1999; Hanski & Ovaskainen, 2000). Saura and Pascual-Hortal (2007) and Drielsma, Manion, and Ferrier (2007) extended this approach and adopted a network-based ecological distance based on the least cost between source and target (d_{st}^{LC}): $k_{st} = \exp(-\alpha d_{st}^{\text{LC}})$. This change drastically altered the behavior of the metrics as it accounted for the role of intervening areas as connectors or "stepping stones" between s and t (Saura et al., 2014; Saura & Rubio, 2010). We suggest the further extension of these metapopulation approaches using the randomized shortest paths framework from network sciences (RSP; Kivimäki et al., 2014; Saerens et al., 2009), which interpolates between optimal and random movement using a "randomness" parameter (θ). More formally, the RSP framework defines a distribution over all paths between s and t. For $\theta \to 0$ this RSP distribution converges to the random walk distribution, whereas the RSP distribution converges asymptotically to

the least-cost path(s) as θ increases (the rate of convergence depends on both the cost units and the size of the graph). In other words, as θ increases, the RSP distribution increasingly focuses on paths with a lower cost. Therefore, the RSP framework simultaneously addresses the cost and the number of paths between two areas for intermediate values of θ (Van Moorter et al., 2021).

Different ecological distance metrics can be defined based on the RSP framework (Van Moorter et al., 2021). Here, we focused on the RSP expected cost (d_{st}^{EC}), which is the cost of paths between s and t multiplied by their likelihood from the RSP distribution. The d^{EC} interpolates between the "commute cost" of the random walk (which is equal to the "resistance distance" up to a constant) for $\theta \to 0$ and the cost of the least-cost path for $\theta \to \infty$. For discussion of other proximity/distance metrics, such as survival probability, we refer to Fletcher et al. (2019) and Van Moorter et al. (2021).

In summary, functional habitat is the summation or eigenvalue/eigenvector of the landscape matrix **M**, in which the elements in the landscape matrix are the product of the suitability of each pair of landscape units ($q_s \times q_t$) multiplied by their proximity (e.g., from the RSP expected cost: $k_{st} = \exp(-\alpha d_{st}^{EC})$, with $k_{st} = 1$ for $s = t$), given a value of θ. The sum of all elements or the leading eigenvalue measures the functionality of the habitat for a whole landscape, whereas the column- or row-wise summation and the right or left eigenvector quantify functional habitat for each mapping unit as a source or target, respectively (Figure 3; see also Appendix S1: Section S1.2 for more details).

Demonstrations

Simulation

We illustrate the response of functional habitat to habitat loss and fragmentation through a landscape of uniformly suitable habitat with different levels of habitat area loss (0%, 44%, and 75% loss) and fragmentation (one, four, and nine habitat patches) in a factorial design (see Figure 4). We computed functional habitat using the RSP expected cost, both at the pixel (Equation 3) and the landscape level (Equation 1).

European wild mountain reindeer

Data

The European distribution of wild mountain reindeer is restricted to the mountain ranges of southern Norway (Figure 5). Due to infrastructure development in the past century, the previously continuous ranges have been fragmented, and reindeer are currently divided into 24 isolated subpopulations (Panzacchi et al., 2015). We have previously used a large amount of environmental data and GPS-tracking data from the 10 largest reindeer management areas, which represent about 65% of the species' range, to investigate reindeer use of environmental space through resource selection functions (Panzacchi et al., 2015) and step selection functions (Panzacchi et al., 2016). Both models have been updated with newly available data and their results and predictions can be explored in a dedicated web app (Panzacchi et al., 2022, 2023). To study reindeer use of geographic space, we used those same GPS-tracking data together with the population estimates presented in Nilsen and Strand (2018), produced by integrating different population-level monitoring data: (1) aerial population surveys during February–March, aiming to exhaustively count each individual in the population (i.e., minimum counts); (2) age–sex data from harvested animals in fall; (3) and surveys of population structure after calving (early summer) and after the hunting season (late fall).

Analysis

We compared functional and suitable habitat in explaining the distribution of wild mountain reindeer (Figure 5A,D). Here, we describe the three parts of our analytical workflow: (1) the estimation of suitable and functional habitats from environmental (E-space) and topological space (T-space), respectively (see Figure 3); (2) the estimation of the reindeer distribution in geographic space (G-space); and (3) the comparison of suitable versus functional habitat (from part 1) to predict reindeer distribution (from part 2). By separating our analysis in E-space and G-space, we were able to avoid circularity from using the same GPS-tracking data for both parts of our analysis.

First, in E-space (see Figure 3), we used the resource selection function (RSF) and step selection function (SSF) from earlier work (respectively, Panzacchi et al., 2015, 2016) to characterize respectively the likelihood of selecting a pixel i as a proxy for its suitability (q_i) and its permeability to the movement (a_{ij}). See Figure 5 for the predicted maps of suitable habitats from the RSF (Figure 5B) and permeable habitats from the SSF (Figure 5C). Unfortunately, we could not directly estimate the cost of movement between adjacent pixels c_{ij}, as we did not have access to data on energy expenditure, and the mortality of marked individuals was virtually zero. Therefore, we assumed that the cost of movement would be a decreasing function of the SSF; more precisely, we assumed a logarithmic relationship ($c_{ij} = -\log(a_{ij})$).
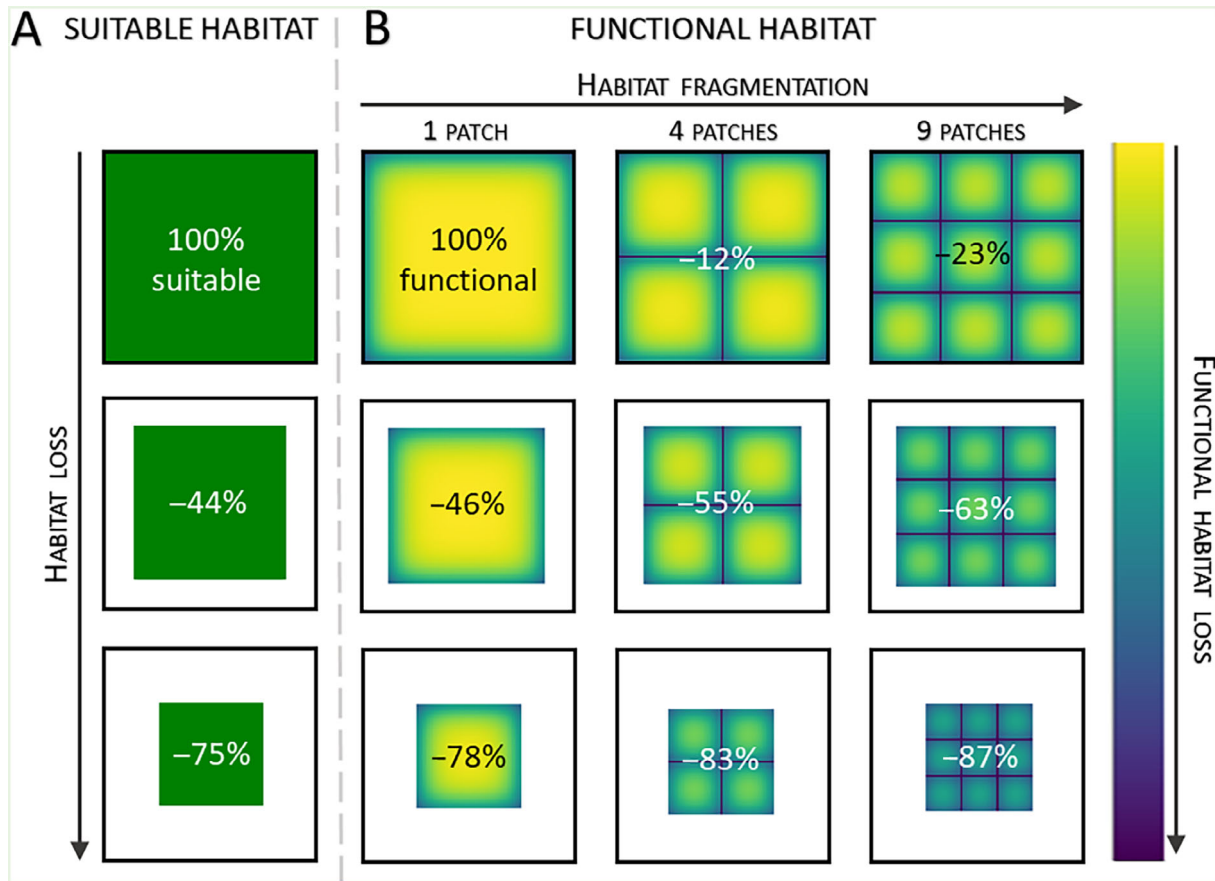
FIGURE 4 Impact of habitat loss and fragmentation on suitable and functional habitats. We used simulations to illustrate the response of suitable (panel A) and functional (panel B) habitat to loss of suitable habitat (along the *y*-axis) and to loss of connectivity (fragmentation along the *x*-axis), occurring separately or simultaneously. The upper square in panel (A) and upper-left one in panel (B) show for the same pristine reference landscape the amount of suitable and functional habitats, respectively. In each row, we reduce the amount of habitat from 0%, 44%, to 75% habitat loss. While for each row in panel (B) we keep the amount of habitat constant, across columns we increase the level of fragmentation from 1 to 4 and 9 fragments. The figure shows that, while the amount of suitable habitat remains constant in each row and does—by definition—not change with fragmentation, the amount of functional habitat reduces in response to both habitat loss and fragmentation.

In addition to the landscape graph, two other parameters affect the ecological proximity between areas in T-space: the randomness of the movement θ and the distance scaling parameter α (Van Moorter et al., 2021). We evaluated $\theta \in (1.0, 0.1, 0.001)$, which covers the continuum from nearly optimal to virtually random. The proximities between pairs of locations were computed using an exponential decay of the RSP expected cost ($\mathbf{K} = \exp(-\alpha\Delta)$). For comparison with earlier work, we also used proximities based on least-cost and Euclidean distances for the landscape matrix. We used four different distance scaling values (α) to represent a range of movement capabilities or neighborhood sizes from more global to more localized ($\alpha \in (1, 1.5, 2, 3)$); the distance scaling was applied after the distances were standardized using two points 32 km apart in the central area of the largest continuous reindeer area (hence, these two points had a proximity k_{st} for

the different values of α, respectively: 0.37, 0.22, 0.14, 0.05). In other words, for the Euclidean distance, the neighborhood ($K > 0.05$) for these four values of α had a radius of about 100, 65, 50, 30 km, respectively. From the landscape matrix we computed functional habitat for each 200 m pixel based on summation, as eigenanalysis for such large landscapes was computationally not feasible.

Second, to estimate the reindeer distribution in G-space, we adapted the weighted kernel utilization density (kernelUD) estimator approach from Fieberg (2007) to account for the spatial stratification of our sample. The GPS-tracked individuals were randomly sampled from each population (of females), however the number of marked individuals was not necessarily proportional to the population size. As sampling was spatially stratified, following Fieberg (2007), we weighted the kernelUD from each population with the average estimated annual
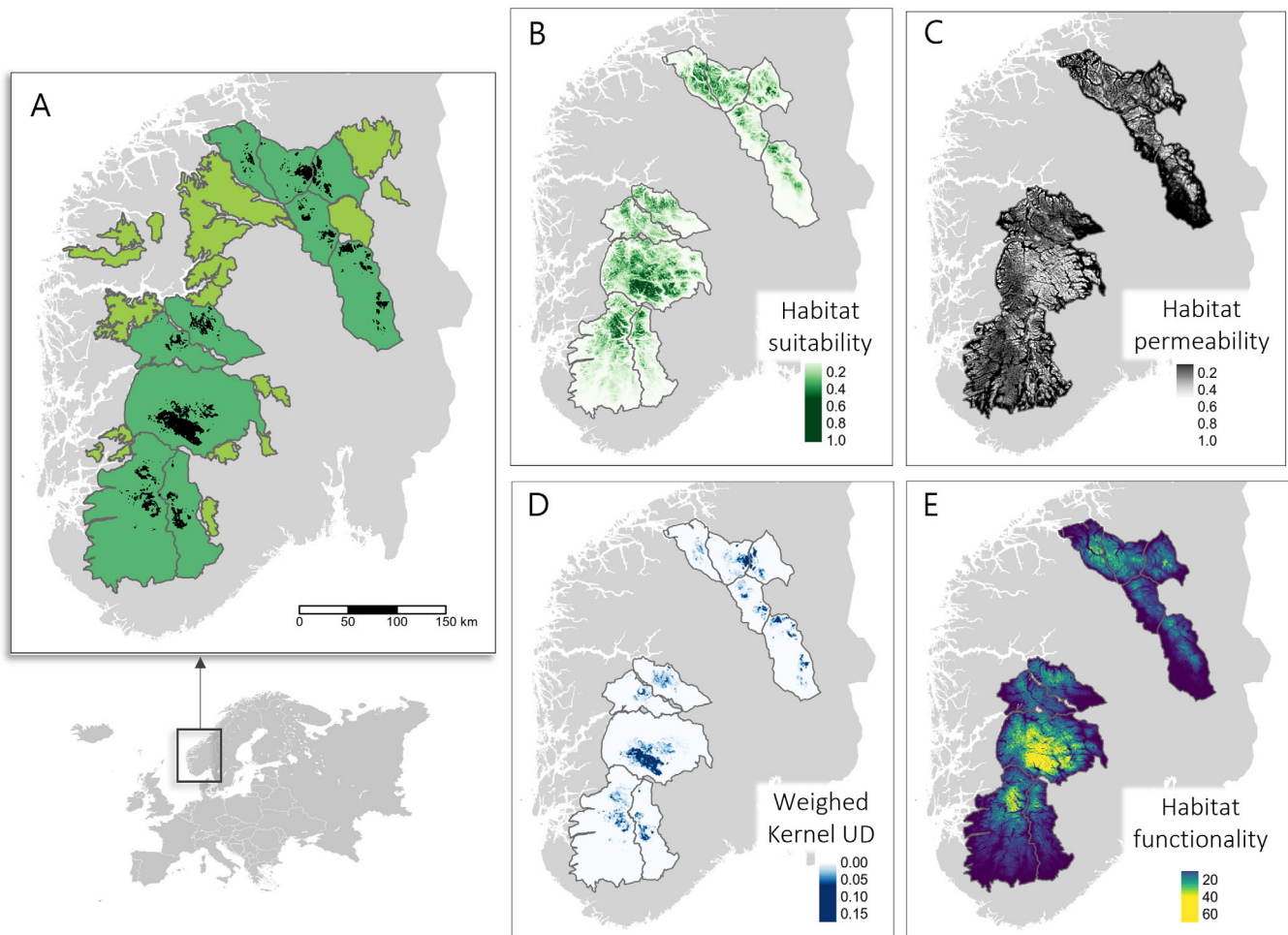
FIGURE 5 The last remaining populations of wild mountain reindeer in Europe are found in Norway and, due to fragmentation, are now subdivided into 24 management units (all green areas [A]). The black points depict the GPS-tracking data used in this study, referring to 10 of the largest management units (dark green; A), during the summer. Panels (B) and (C) show the summer maps of habitat suitability and of permeability, respectively, used in this study as input to estimate functional habitat (panel E; Figure 3). Panel (D) illustrates the kernel utilization distribution, weighted by population size.

population size from Nilsen and Strand (2018). For each individual, we computed the kernelUD from the GPS-tracking data. These individual-level kernelUDs were combined into subpopulation-level kernelUDs by summing the individual kernelUDs from each individual in the subpopulation. The population-level distribution was then computed as the weighted sum of the subpopulation-level kernelUDs, weighted by the size of the subpopulation. We obtained the index for population size through data integration by combining population counts, harvest statistics, and population structure from Nilsen and Strand (2018), see details therein.

Finally, we tested the ability of suitable versus functional habitats to explain the distribution of wild mountain reindeer in our study areas. The habitat suitability of each pixel was estimated using RSFs (Panzacchi et al., 2015). As discussed above, we included several variants of functional habitat. As the distribution of reindeer was heavily

zero-inflated, that is >65% of pixels were not occupied by reindeer, we opted to fit it with a hurdle model. Hurdle models are often used for zero-inflated abundance data, where the full model consists of two parts: an occurrence model describing presence/absence, and an abundance model describing variability in abundance for nonzero data (Zeileis et al., 2008). The log-likelihood of these two parts can be combined to assess the likelihood of the full hurdle model. The occurrence part of the hurdle model was fitted using logistic regression, while the abundance part was fitted using linear regression. We then tested the ability for suitable habitat (in E-space), the neighborhood habitat suitability index (NHI; using different α values for the exponential decay of the Euclidean distance), and functional habitat with the RSP expected cost (using different θ and α parameters, see above) and with the least cost (equivalent to RSP expected cost, with θ → ∞) to explain the population distribution. Both the NHI and functional habitat

values were square-root transformed, as the environmental suitability of both the source and target nodes are multiplied for their computation, for example, Equation (3). This transformation is similar to the one in Saura et al. (2011), to compute the "equivalent connected habitat" (see Van Moorter, Kivimäki, Noack, et al., 2023 for further discussion). Our aim was not to obtain the best possible parameter estimates, but rather to test which variable best explains the spatial patterns of population abundance. Therefore, we did not include a latent variable to account for spatial autocorrelation, as this could artificially improve the apparent performance of a variable. We compared models using AIC and sum-of-squared-residuals (SSR).

For our demonstration, we focused our analysis on the summer period (1 July to 15 August), as during the summer reindeer are most affected by habitat fragmentation due to both natural sources of fragmentation (e.g., lakes are not frozen) and human disturbances (e.g., due to recreational use of the mountains during the holiday period). Except for one out of the 10 subpopulations, the seasonal ranges showed clear overlap. We therefore did not consider connectivity among seasonal habitats as a major issue for the purpose of this study, as the animals were able to access the seasonal habitat available for each subpopulation. As subpopulations are determined based on their isolation from each other, we analyzed the functional habitat for each subpopulation separately. Network analyses were conducted in Julia software (Bezanson et al., 2017) using the ConScape-library (Van Moorter, Kivimäki, Noack, et al., 2023), whereas all other analyses were performed in R (R Core Team, 2015).

RESULTS

Simulation

Figure 4 shows that functional habitat responds to both habitat loss and fragmentation (see also: Rubio & Saura, 2012), whereas habitat suitability in E-space ignores—by definition—the fragmentation of the landscape. Hence, functional habitat allows for the integrated assessment of habitat loss and fragmentation. Figure 4 shows that the impact of habitat loss on functional habitat increases in the presence of habitat fragmentation, which has significant consequences for impact assessment and sustainable land planning.

European wild mountain reindeer

In G-space, we estimated the kernel utilization distribution (kernelUD; Calenge, 2006) from the GPS-tracking data for each individual. The average smoother (h) from the least-squares cross-validation for each individual was 386. We added these individual kernelUDs to compute the utilization distribution for each subpopulation. These subpopulation UDs were added after weighing using the population size index. By weighing the UDs with the population size, the volume under each subpopulation's utilization distribution was proportional to its size; hence, we can consider Figure 5D an estimate of the reindeer distribution across the monitored areas.

Table 1 shows the comparison of suitable habitat ($\mathcal{S}$) and functional habitat ($\mathcal{K}$) in explaining reindeer distribution. Overall, the reindeer distribution was best explained by $\sqrt{\mathcal{K}}$ with $\theta = 0.001$ (relatively random movements) and $\alpha = 3$ (a neighborhood size of about 30 km). Model performance dropped first with increasing neighborhood size; within each neighborhood size the models were ranked based on their randomness, suggesting that animals are investing in exploring their environment. Most versions of functional habitat ($\mathcal{K}$ and NHI) outperformed the model based on suitable habitat $\mathcal{S}$, only functional habitat computed with very large neighborhood sizes (100 km) performed worse. Interestingly, the performance of the metrics on the subcomponents of the hurdle model (occurrence and abundance) mirrored the results of the full model for the neighborhood size α. However, different variants of functional habitat performed better at the different parts of the hurdle model. The occupancy part of the hurdle model was best explained based on the Euclidean distance in the $\sqrt{\text{NHI}}$ followed by intermediate values of randomness θ for $\sqrt{\mathcal{K}}$, while the abundance part was best explained based on the least-cost distance followed by more random values of θ (actually, Euclidean distance performed poorly on the abundance part). While the models with functional habitat consistently outperformed those with suitable habitat, the differences in the sum-of-squared-residuals are small (see Table 1). This is not surprising given the similarity between these habitat metrics (see Figure 5B,E), Spearman's correlation between $\mathcal{S}$ and $\sqrt{\mathcal{K}}$ ($\theta = 0.001$ and $\alpha = 3$) is very high ($r > 0.92$).

DISCUSSION

The "functional habitat" niche framework formally integrates the suitability of habitat in environmental space (E-space) with its accessibility in geographic space (G-space) using advances in landscape ecology and network sciences, in topological space (T-space). The prediction (in G-space) of a species' niche (defined in E-space), hereafter referred to as "suitable habitat" (Hirzel & Le Lay, 2008), ignores topological relationships between areas. However, virtually all authors agree that ignoring spatial relationships is merely a simplification dictated by the lack of an

TABLE 1 Comparison of models for reindeer distribution based on suitable versus functional habitat.

Variable[a]	θ	α	Zero density Coefficient	SE	ΔAIC	Nonzero density Coefficient	SE	ΔAIC	Combined %ΔSSR[b]	ΔAIC[c]
$\sqrt{\mathcal{K}}$	0.001	3	1.06e-01	2.62e-04	1699	8.44e-04	2.84e-06	906	0.01	0
$\sqrt{\mathcal{K}}$	0.1	3	1.03e-01	2.56e-04	710	8.14e-04	2.76e-06	2318	0.07	423
$\sqrt{\mathcal{K}}$	1.0	3	1.05e-01	2.64e-04	2997	8.19e-04	2.76e-06	1058	0.04	1451
$\sqrt{\mathrm{NHI}}$		3	9.66e-02	2.36e-04	0	7.84e-04	2.73e-06	5971	0.29	3367
$\sqrt{\mathcal{K}}$	∞	3	1.08e-01	2.74e-04	6836	8.32e-04	2.78e-06	0	0.00	4231
$\sqrt{\mathcal{K}}$	1.0	2	7.54e-02	1.94e-04	19,119	6.14e-04	2.13e-06	5046	0.76	21,560
$\sqrt{\mathcal{K}}$	0.1	2	7.33e-02	1.88e-04	20,329	6.09e-04	2.12e-06	5970	0.81	23,695
$\sqrt{\mathcal{K}}$	0.001	2	7.40e-02	1.90e-04	22,293	6.24e-04	2.16e-06	4955	0.81	24,643
$\sqrt{\mathcal{K}}$	∞	2	7.64e-02	1.99e-04	22,975	6.20e-04	2.14e-06	4495	0.77	24,865
$\sqrt{\mathrm{NHI}}$		2	6.92e-02	1.75e-04	21,568	5.92e-04	2.10e-06	8315	0.94	27,278
$\sqrt{\mathcal{K}}$	1.0	1.5	6.08e-02	1.60e-04	31,444	5.16e-04	1.81e-06	7220	1.24	36,059
$\sqrt{\mathcal{K}}$	∞	1.5	6.06e-02	1.62e-04	37,243	5.17e-04	1.82e-06	7117	1.32	41,756
$\sqrt{\mathcal{K}}$	0.1	1.5	5.83e-02	1.54e-04	36,373	5.10e-04	1.81e-06	8180	1.35	41,948
$\sqrt{\mathcal{K}}$	0.001	1.5	5.85e-02	1.55e-04	38,591	5.19e-04	1.83e-06	7430	1.38	43,416
$\sqrt{\mathrm{NHI}}$		1.5	5.55e-02	1.45e-04	38,374	4.98e-04	1.79e-06	9888	1.45	45,657
$\sqrt{\mathcal{K}}$	1.0	1	4.72e-02	1.27e-04	46,677	4.23e-04	1.51e-06	9413	1.81	53,485
$\mathcal{S}$			6.69e+00	1.86e-02	55,424	5.76e-02	2.10e-04	12,035	1.69	64,854
$\sqrt{\mathcal{K}}$	∞	1	4.54e-02	1.25e-04	57,424	4.19e-04	1.51e-06	10,089	2.04	64,908
$\sqrt{\mathcal{K}}$	0.1	1	4.39e-02	1.20e-04	58,145	4.14e-04	1.50e-06	10,826	2.07	66,366
$\sqrt{\mathcal{K}}$	0.001	1	4.38e-02	1.21e-04	60,227	4.18e-04	1.51e-06	10,362	2.12	67,984
$\sqrt{\mathrm{NHI}}$		1	4.22e-02	1.15e-04	60,551	4.06e-04	1.48e-06	11,975	2.16	69,922

Abbreviations: %ΔSSR, percentage increase in the sum-of-squared-residuals compared to the minimum value; ΔAIC, difference in AIC between models.

[a]Three types of variables were used to explain reindeer distribution: habitat suitability ($\mathcal{S}$), neighborhood habitat index (NHI; Hanski, 1999), and functional habitat ($\mathcal{K}$) using a range of θ-values (θ $\in$ [∞, 1.0, 0.1, 0.001], where ∞ corresponds to the least-cost distance); for both NHI and **K** we used several distance scaling factors ($\alpha \in$ [1, 1.5, 2, 3]). The NHI and **K** values were square-root transformed to obtain a value similar to the "equivalent connected habitat" (Saura et al., 2011; Van Moorter, Kivimäki, Noack, et al., 2023).

[b]Percentage increase in sum-of-squared-residuals (SSR) compared with the minimum value.

[c]ΔAIC based on the combined log-likelihood from both hurdle components.

adequate framework, and recognize that species' movements do shape their geographic distribution (Soberon & Peterson, 2005). Indeed, the failure to account for spatial relationships contributes to the mismatch often observed between species' distributions and their fundamental niche, fueling a debate about the utility of the niche concept in nature management and conservation (e.g., Angilletta Jr. et al., 2019; Matthiopoulos, 2022). Indeed, for management applications, Hirzel and Le Lay (2008) recommended to "consider discarding suitable patches that are too small," in recognition of the fact that the viability of an area for a species does not exclusively depend upon E-space, but also upon its size, accessibility, and centrality (Figure 1).

Building upon approaches from metapopulation and network theory, the "functional habitat" niche framework formally reconnects the E-space and G-space by representing the niche in T-space, including not only local biotic and abiotic characteristics, but importantly also the functional connectivity between suitable habitat areas. Indeed, the development of the functional habitat framework has been largely driven by the need to produce a theoretically sound modeling approach to support sustainable land planning for conservation (e.g., Panzacchi et al., 2022, 2023). In the popular BAM (biotic–abiotic–movement) niche framework (Soberon & Peterson, 2005), the concept of functional habitat corresponds to areas that are simultaneously suitable due to appropriate biotic and abiotic conditions, and functionally connected, that is, accessible through movement (Figure 1). Functional habitat is analogous to what has

been called the "actual distribution" (in contrast to the potential distribution) in the context of species distributions (Soberon & Peterson, 2005), but it can also be applied at smaller scales, such as population or individual ranges. The functional habitat definition implies that, if there is no fragmentation and movements are not hampered (movement cost $\mathbf{C} = 0$), functional habitat would correspond to suitable habitat (Figure 4). However, if landscape permeability to movements is limited (i.e., $\mathbf{C} > 0$), the amount of functional habitat in a landscape becomes smaller than the amount of suitable habitat. The differences between functional and suitable habitat increases as landscape permeability decreases, and is highest in the extreme case where impermeable barriers block movements between suitable habitat patches. This has major implications for species' management, as sustainable land planning cannot continue to ignore the highly interdependent and often multiplicative effects of habitat loss and fragmentation (Figure 4).

Using the ConScape-library (Van Moorter, Kivimäki, Noack, et al., 2023; Figure 3), we computed the functional habitat for reindeer in Norway, and we tested its performance in describing the population distribution of wild mountain reindeer. Specifically, we predicted that functional habitat would be better able to describe population distribution compared with traditional suitable habitat throughout the European distribution range of wild reindeer (Figure 5). In support of our hypothesis, we found that functional habitat in T-space explained reindeer distribution better than the mere suitability of the local habitat in E-space. This result was consistent for virtually all variants of functional habitat tested, that is, using different levels of randomness in the movement and selecting different neighborhood sizes. However, as expected, the differences between functional and suitable habitats were relatively small (1%–2%). Two main factors contributed to these small effect sizes: first, functional habitat is a subset of suitable habitat (Figure 1), and these two metrics are therefore necessarily strongly correlated ($r > 0.92$). Second, suitable habitat was estimated here using a conditional logistic regression to fit an RSF classifying used and available locations within each herd (Panzacchi et al., 2015). In other words, the RSF was explicitly trained to explain the population distribution within each herd, while functional habitat was not. Hence, our test was very conservative. Future research could investigate the direct estimation of the species' landscape network based on occurrence and movement data to allow for a more accurate comparison of suitable and functional habitats. For instance, the integrated step selection analysis (Avgar et al., 2016; Beyer et al., 2016) and the MCMC step selection models (Michelot et al., 2019, 2020) are promising developments in this direction.

By definition, the difference between suitable and functional habitats increases as landscapes become more fragmented and less permeable to the movement of organisms (Figure 4). However, fragmentation and landscape permeability are species and process dependent, mediated by life history characteristics ("functional connectivity for whom?" Ewers & Didham, 2006; Tischendorf & Fahrig, 2000). Traits, such as body size, trophic level, mobility, and dispersal ability, sociality, diet breadth, and generation time are known to affect species responses to habitat fragmentation (Amburgey et al., 2021; Barbaro & Van Halder, 2009; Ewers & Didham, 2006) and are likely to strongly influence functional habitat. As landscapes get more fragmented for a species and process, due to barriers that hinder movements and establishment in new areas, the difference between suitable and functional habitats is expected to increase, making the latter increasingly more important for species and landscape conservation.

Effective connectivity is dependent upon the focal ecological process (i.e., "connectivity for what?" Fletcher et al., 2016; Van Moorter et al., 2021). The first metrics to assess the amount of connected habitat were developed focusing on metapopulation dynamics (Hanski, 1999; Hanski & Ovaskainen, 2000), that is, on the likelihood of colonization through dispersal movements. In our demonstration, we focused on daily movements and on the functional connectivity within reindeer summer ranges, which is highly relevant for conservation and land planning due to the large amount of transportation and touristic activities that hamper reindeer movements in that season. We did not focus on other processes such as seasonal migration, dispersal, or colonization, as most migration routes have been lost in the past century, and the current reindeer range is highly fragmented (Panzacchi et al., 2016). However, our approach is highly flexible and suitable to assess functional connectivity focusing on a range of ecological processes such as migratory movements, colonization, and dispersal, which are important for a range of other species, including several other *Rangifer* subspecies (Vors & Boyce, 2009). Indeed, the integration of the randomized shortest path algorithm within the functional habitat framework allows taking into account both the number of alternative paths and the cost of paths between functional area units (Van Moorter et al., 2021), thus providing a flexible framework applicable to a variety of movement patterns and ecological processes (e.g., metapopulation dynamics).

One of the strengths of the proposed approach is that the landscape network can be parameterized using empirical, high-resolution animal movement data from GPS collars (see also: Van Moorter et al., 2021). Both suitability and permeability of habitat were estimated explicitly using RSFs and SSFs, respectively (Panzacchi

et al., 2015, 2016). This allowed us to make data-driven inferences regarding the functionality of specific landscape elements in our study area (Chetkiewicz & Boyce, 2009). However, note that movement data are not strictly necessary to compute functional habitat, which can be computed based on the proxies of suitability and permeability. For instance, in the absence of movement data, occurrence data can provide a useful estimation of genetic connectivity between populations (Zeller et al., 2018). Similarly, functional habitat for forest-dwelling and wetland-dwelling species could be calculated through expert-based classification of the quality and permeability of land cover classes, and information on the species' movement characteristics (e.g., Koen et al., 2014; Stange et al., 2019).

This network-based habitat functionality approach allows a high degree of flexibility in the representation of the spatial configuration of landscape elements. Hence, landscapes can be modeled in relatively realistic ways, including (semipermeable) barriers to movement, which contributes to its potential to concretely guide sustainable land planning. The amount of functional habitat in a given landscape can be synthesized into one number, which integrates the amount and connectivity of suitable habitat; thus, the amount of functional habitat can be compared among current, past, or alternative landscape scenarios. This is particularly useful in studies of cumulative impact assessments, to quantify the effect of anthropogenic land use or climate change, or to rank the expected effect of mitigation measures and off-set actions. As habitat functionality operates in T-space, and is able to account for changes in the spatial configuration of a multitude of landscape elements simultaneously (including infrastructures representing barriers to movements, changes in land use, tourism development, etc.), the sustainability of entire land plans can be assessed. The habitat functionality framework is currently being tested to support sustainable land planning and the identification of the most efficient mitigation measures in Norwegian wild reindeer areas, focusing on issues such as hydropower development, transportation, and tourism (Dorber et al., 2023; Panzacchi et al., 2022, 2023).

Previous approaches to include movement constraints into species distribution models have focused on connecting the current species' distribution range to future predicted suitable habitat and using, for instance, scenarios of climate change (e.g., Bateman et al., 2013; Engler et al., 2012; Holloway et al., 2016). These approaches have relied upon either some forms of dispersal kernel based on Euclidean distances or on some estimates of ecological distances (Landguth et al., 2017; Miller & Holloway, 2015). The network-based approach presented in this paper can be used to estimate the functional connectivity between

the current range and the forecasted suitable habitat. Specifically, in Equation (4), q_s would then represent the current occupancy of a source pixel and q_t the forecasted future suitability of a target pixel, which would allow the assessment of functional habitat over longer time scales.

A major area for future research is the link between functional habitat and population dynamics. Recently, Matthiopoulos (2022) has proposed a mathematical framework for augmenting E-space to incorporate spatial relationships in niche models, which allows bridging the gap between habitat and demography. While this augmented E-space is conceptually powerful and is not a mathematical problem, "the curse of dimensionality" is however a real statistical one (Matthiopoulos, 2022). This is likely to limit the applicability for such an approach for applied land-planning studies with many different landscape features and complex configurations, especially in situations in which barriers play a significant role in shaping movements. The functional habitat approach is computationally less demanding and can be efficiently computed using the ConScape-library (Van Moorter, Kivimäki, Noack, et al., 2023) for large, high-resolution landscapes. Therefore, it can support future developments linking complex landscape patterns to demography and population dynamics.

CONCLUSION

The functional habitat framework is a step toward the integration of E-space and G-space into the environmental niche concept, thus allowing researchers to model connected habitat in T-space functionally and effectively. From an empirical perspective, functional habitat proved to be robust in describing the population distribution of wild mountain reindeer throughout their European distribution range, outperforming traditional suitable habitat metrics. From a theoretical perspective, the framework builds on metapopulation theory, including more flexible assumptions and broadening its applicability. By integrating the effects of both habitat degradation and loss of connectivity or fragmentation into a quantitative metric (Rubio & Saura, 2012), the habitat functionality framework goes beyond simplistic dichotomies that might hinder conservation practice (whether to manage single large or several small habitat patches; Riva & Fahrig, 2023; Szangolies et al., 2022) and has great potential to guide sustainable land planning. This makes the framework ideally suitable for assessing the cumulative impacts of anthropogenic activities, including infrastructure development, land-use changes and climatic changes (Dorber et al., 2023). The concept of a functionally connected niche is fundamental for better describing

current species distributions, and it is essential for predicting how species' distribution could respond to climatic or landscape changes. The functional habitat framework we propose will enable researchers to address both these aspects with a high level of realism in the representation of species' movements. Finally, its computational efficiency enables it to be operated in large, high-resolution landscapes (Van Moorter, Kivimäki, Noack, et al., 2023), thus addressing one of the most challenging demands from conservation and management.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data and scripts are available in a Dryad repository (https://doi.org/10.5061/dryad.dfn2z354x; Van Moorter, Kivimäki, Panzacchi, et al., 2023). The code for the computation of functional habitat (provided in Van Moorter, Kivimäki, Panzacchi, et al., 2023) is based upon the ConScape library and the codes—presented as notebooks with documentation—in the supplementary material of Van Moorter, Kivimäki, Noack, et al. (2023) with only minor modifications.

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SUPPORTING INFORMATION

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