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Identification and prioritization of stepping stones for biodiversity conservation in forest ecosystems

Katharina Lapin | **Johanna A. Hoffmann** | **Martin Braun** | **Janine Oettel**

Department of Forest Biodiversity and Nature Conservation, Austrian Research Centre for Forests, Natural Hazards and Landscape (BFW), Vienna, Austria

Correspondence
Katharina Lapin, Department of Forest Biodiversity and Nature Conservation, Austrian Research Centre for Forests, Natural Hazards and Landscape (BFW), Seckendorff-Gudent-Weg 8, 1131 Vienna, Austria.
Email: katharina.lapin@bfw.gv.at

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Abstract

Habitat degradation and fragmentation are two of the main drivers for biodiversity loss. To mitigate the negative impact of fragmentation in forests, conservation targets are increasingly addressing connectivity to facilitate the independent movement of species between habitat fragments to ensure genetic diversity and adaptation to climate change. In this article, we present a novel approach to identifying and prioritizing stepping stones for preserving connectivity based on national and regional biodiversity data for Austrian forest ecosystems. Our study identified forest areas where conservation measures should be taken to ensure future habitat connectivity by combining four indicator values with different requirements of a stepping stone habitat into a prioritization value. The four compounded indicators are: (i) the *Protect Value*, which includes distances to patches of protected areas with restricted management for the undisturbed development of retention areas, (ii) the *Connect Value*, which combines datasets of designated habitat corridors and connectivity areas in Austria based on landscape models and expert validation, (iii) the *Species Value* identifying species-rich areas, and (iv) the *Habitat Value* identifying biotopes of high ecological value, key biodiversity areas, and sites of favorable protection status. Nonparametric tests revealed significant differences in prioritization value among the ecoregions of Austria and therefore encourage the consideration of stepping stone prioritization at local and regional context. Building upon the insights from this case study on Austrian forest ecosystems, we developed a robust framework derived from our methodology. This framework is designed to facilitate future implementations in diverse study regions, accounting for factors beyond connectivity crucial for identifying high value stepping stone habitats. We encourage adaptation of this framework to local data availability, species requirements, and local conditions. The compiled framework provides decision support for managers and conservationists for prioritizing areas to conserve and improve connectivity of forest habitats.

However, it does not substitute on-the-ground field assessments of habitat quality and measures of functional connectivity.

KEYWORDS

biodiversity, connectivity, forest conservation, protected areas, spatial conservation, species migration, species richness, stepping stone habitats

1 | INTRODUCTION

Fragmentation of forests, considered a major risk to biodiversity, is driven primarily by habitat fragmentation and ecosystem degradation globally. This loss of biodiversity poses a significant challenge for human society to address in the 21st century (Cardinale et al., 2012; Watson et al., 2019). Habitat fragmentation describes the effects of a reduction in available habitat area combined with increased isolation of habitat patches on biodiversity (Fahrig, 2003). Isolation refers to distance as well as to how easy it is for species to move through the landscape. Linear infrastructures such as roads or railways are the primary impediments to species movement and also increase mortality rates for many species (Brotons & Herrando, 2001; Tellería et al., 2011). The road network in a landscape provides a good proxy for the degree of fragmentation of a landscape (Bennett, 2017). Altering the quality and connectivity of habitats results in reduced species dispersal and gene flow (Wilson et al., 2016), which in turn leads to limitations regarding species adaptation to climate change (Krosby et al., 2010; Sonntag & Fourcade, 2022) and consequently to species extinction (Cheptou et al., 2017; He et al., 2018; Ntshanga et al., 2021; Theodoridis et al., 2021). Over the next 100 years, with a projected temperature rise of 1.1–5.4°C (2–9.7°F) (Meehl et al., 2007), range shifts are expected for most species. Improving the ability of species to move to new areas has consequently become a widely accepted target for conservation management and climate change adaptation (Hijmans et al., 2005).

At the global level, 70% of the total forest area has been shown to be less than 1 km from a forest edge, leading to a decline in species richness (Krosby et al., 2010; Pfeifer et al., 2017). Forest edge distance characterizes the type of interfaces between forested and non-forested land depending on the type of land cover at the edges. Forest edges in natural or seminatural areas can be distinguished from forest edges with a more anthropogenic pattern. Following Estreguil et al. (2013), 60% of forest edges in the European Union are located along intensively used land; In general, edge effects are caused by abiotic and biotic changes at the interface of adjacent areas of different land cover (Fischer & Lindenmayer, 2007) and exacerbated at interfaces with a strong contrast between land cover types. Edge density refers to the number of habitat edges per unit of area and is influenced by the size and shape of a habitat (Soifer et al., 2021).

Forest fragmentation is primarily measured as a change in forest cover over time—the result of a human-induced or disturbance-driven process of partitioning of forested areas into smaller and more isolated patches (Kim et al., 2012; Lindenmayer & Fischer, 2013; Saunders et al., 1991). To mitigate the negative impact of fragmentation, forest conservation targets increasingly address connectivity to facilitate the independent movement of species and gene flow between habitat patches and along corridors (Crooks & Sanjayan, 2006; Rudnick et al., 2012; Worboys et al., 2010).

Management actions to increase connectivity and facilitate the movement of species include the establishment of corridors between protected areas or biodiversity hotspots as well as stepping stone reserves (hereafter: stepping stones) (Krosby et al., 2010).To combat fragmentation, the concept of connectivity has been developed since the 1970s. Taylor et al. (1993) defined connectivity as the degree to which a landscape facilitates or impedes movement among resource patches, encompassing the spatial distribution of patches as well as the movement success of species in response to it. In much of the literature on landscape connectivity, movement success is assumed to be closely linked to the spatial distribution of habitats across landscapes, and movement is assumed to be strongly constrained by habitat (Fahrig et al., 2021). This has led to a focus on linear structures (habitat corridors), small patches of temporal habitat (stepping stones), and the distances between habitats (Formann, 1995). Corridors are expected to be advantageous for species that specialize in certain habitats, rely on undisturbed habitats, and have limited mobility. On the other hand, stepping stones may not offer the same physical habitat continuity as corridors, but they can still be beneficial for mobile species and those more resilient to habitat disturbance, as well as for species with wider ranges compared to those that benefit from corridors (With, 2019).

Several studies have illustrated the identification of areas as stepping stones for biodiversity conservation across regional or national boundaries as a practical decision-making tool for conservation planning (Herrera et al., 2017; Molina Sánchez et al., 2019; Schüßler et al., 2020; Wu et al., 2022). However, large-scale analysis of forest habitat connectivity shows differences across ecoregions that should be considered when managing for forest connectivity at the ecoregion scale (Piquer-Rodríguez et al., 2015). Given uncertain future land use patterns, increasing the connectivity of protected areas in different ecoregions through corridors and stepping stones has become a major challenge for biodiversity conservation in the face of climate change (Han et al., 2021; Saura et al., 2017).

Numerous connectivity metrics have been developed to assess the connectivity of ecosystems and identify areas of high conservation priority (Keeley et al., 2021). These connectivity metrics can be summarized into two main concepts: (a) structural connectivity and (b) functional connectivity (Correa Ayram et al., 2016). Structural connectivity metrics refer to the distances of patches or corridors and their spatially explicit patterns such as size, shape, potential buffer area or cohesion (Kindlmann & Burel, 2008). By contrast, functional connectivity metrics are based on the species-specific responses to landscape patterns that affect the population development of a focal species or metapopulations (Laita et al., 2011; Prugh, 2009). Especially during the past decade, more emphasis has been placed on combining the connectivity of landscape pattern with species-specific data (Heintzman & McIntyre, 2021; Petsas et al., 2020) such as dispersal rates, migration capacities, or even genetic diversity (Dutcher et al., 2020; Klinga et al., 2019). However, it is important to highlight that existing approaches for identifying areas crucial for ecological connectivity often lack incorporation of information regarding the habitat quality of these areas. As of now, a methodological framework for the systematic identification of such key areas for the conservation of ecological connectivity remains absent.

Around 35% of the European land area is currently covered with forests (EEA, 2020); these forests have been characterized by human intervention for hundreds of years and are very heterogeneous among the different countries (Pötzelsberger et al., 2021). The share of forests in protected areas in Europe is around 33% (49.3 million ha) (Forest Europe, 2020), and estimations show that only 3% are primary and old growth forests (Sabatini et al., 2018). However, it is expected that protected areas will not be able to mitigate the biodiversity loss under climate change (Hoffmann et al., 2019) without increases to their connectivity among other conservation measures such as in situ and ex situ management of endangered species, biodiversity-friendly forest management, and active monitoring of pests, diseases, and invasive species (Oettel & Lapin, 2020). Development of wildlife corridors and refuges to restore connectivity threatened by climate change has become an important measure for achieving the UN Global Forest Goals (United Nations Department of Economic and Social Affairs, 2021). Under the European Green Deal, the EU Biodiversity Strategy for 2030 and the EU Forest Strategy for 2030 call for increasing the connectivity of forest habitats to restore and conserve biodiversity in the European landscape.

This study develops a novel framework to identifying and prioritizing forested habitats with high relevance for conservation as stepping stones to preserve the ecological connectivity of habitats. The identification and prioritization of forest habitats, in the sense of this study, aims to preserve ecological connectivity by establishing stepping stones and conserving sites with forest structural features of high habitat quality for biodiversity, such as deadwood amount, diverse forest structure, or presence of old trees and tree-related microhabitats. We aim for a robust framework describing forested habitats for conservation planning that is easy to apply, transparent, and based on nationally and regionally accessible biodiversity data. Our specific objectives are to (1) develop such a prioritization framework for forested habitats based on biodiversity data, (2) identify priority areas for conservation as stepping stones to preserve habitat connectivity in Austria, (3) compare the prioritization values across altitudes and ecoregions of Austria, and (4) assess the influence of edge distance, edge density, and distance to the nearest road on the prioritization value. In doing so, our framework provides guidance for land managers, governments, and nongovernment conservation agencies attempting to ensure future connectivity of ecosystems in Central Europe and elsewhere. Specifically, it illustrates the importance of stepping stones as a measure to mitigate and prevent habitat fragmentation beyond the conservation of protected areas.

2 | MATERIALS AND METHODS

2.1 | Study area

Austria is a landlocked country in Central Europe with an area of about 8.34 million ha. It features a forest cover of almost 50%, of which 84% (3.36 million ha) are under management (BFW, 2022; BFW (Bundesforschungszentrum für Wald), 2022). Austrian forests span a wide range of elevations (120–2100 m a.s.l.) and climates (continental Pannonian, Alpine, and transitional central European climates), resulting in a considerable diversity of forest types (and thus tree species compositions) ranging from temperate lowland forests to subalpine forests (Russ, 2019). Around 68,000 species, including 2900 plant species and 54,000 animal species, have been recorded in Austria to date. Insects are the largest taxonomic group, including over 40,000 insect species (Geiser, 2018). In terms of landscape fragmentation, Austria has an absolute area of 29,000 km^2 with high and very high fragmentation (34%) (EEA, 2021), and with 1299 meshes per 1000 km^2, the country is positioned in the upper middle range among European countries. Highly fragmented forest areas amount to 7800 km^2, constituting about 20% of the total forest area in the country.

2.2 | Methodological framework

To develop a prioritization framework and calculate a prioritization metric, we used spatial data and connectivity information and combined it into four indicators: (i) *Protect Value*, (ii) *Connect Value*, (iii) *Species Value*, and (iv) *Habitat Value* (Figure 1). A comprehensive GIS-based spatial analysis was conducted using QGIS (Versions 3.4 and 3.16.11) and its programming environment pyQGIS (Python Version 3.9) to collate the corresponding spatial data of each indicator value (see Appendices 1, 3, 4, 5 for more detailed information). Indicator values as well as the final prioritization value were normalized using pixel-wise min-max standardization resulting in values ranging between 0 and 1. The standardization is represented by this formula:

$$Y = \frac{(x - x_{\min})}{(x_{max} - x_{\min})}$$

with Y being the normalized value of an indicator (protect value, connect value, species value or habitat value) or the final prioritization for each pixel; x being the individual pixel value of the indicators or prioritization, $x_{\min}$ being the minimum value of all indicator or prioritization values, $x_{\max}$ being the maximum value of all indicator or prioritization values.

The *Protect Value* was calculated as the spatial distance to strictly protected areas that restrict management for the undisturbed development of retention areas. These “patches” contain areas of IUCN category I to III (UNEP-WCMC/IUCN, 2022), nature reserves, wilderness areas (Land Steiermark, 2021), locally protected stepping stones (Netzwerk Naturwald, 2022), and natural forest reserves (BFW, 2022; Land Tirol, 2022; ÖBF, 2022) (see Appendix 1). The *Protect Value* describes the priority of a given area within Austria for establishing a stepping stone in terms of its distance to protected areas, with high values indicating high priority.

As the present analysis does not focus on specific species or species groups and maximum dispersal distances vary significantly among different species groups as well as within them (Alex Smith & Green, 2005; Caton et al., 2022; Muller-Landau et al., 2008; Whitmee & Orme, 2013) this indicator instead aims to focus on structural connectivity between protected areas on a national scale. That is why we rated the protect value in a curve according to the value distribution of the distances instead of species dispersal distances from literature. A distance value curve was created in sensu Hanski (1994), which indicates that the probability of species migration has an optimum distance and follows an exponentially

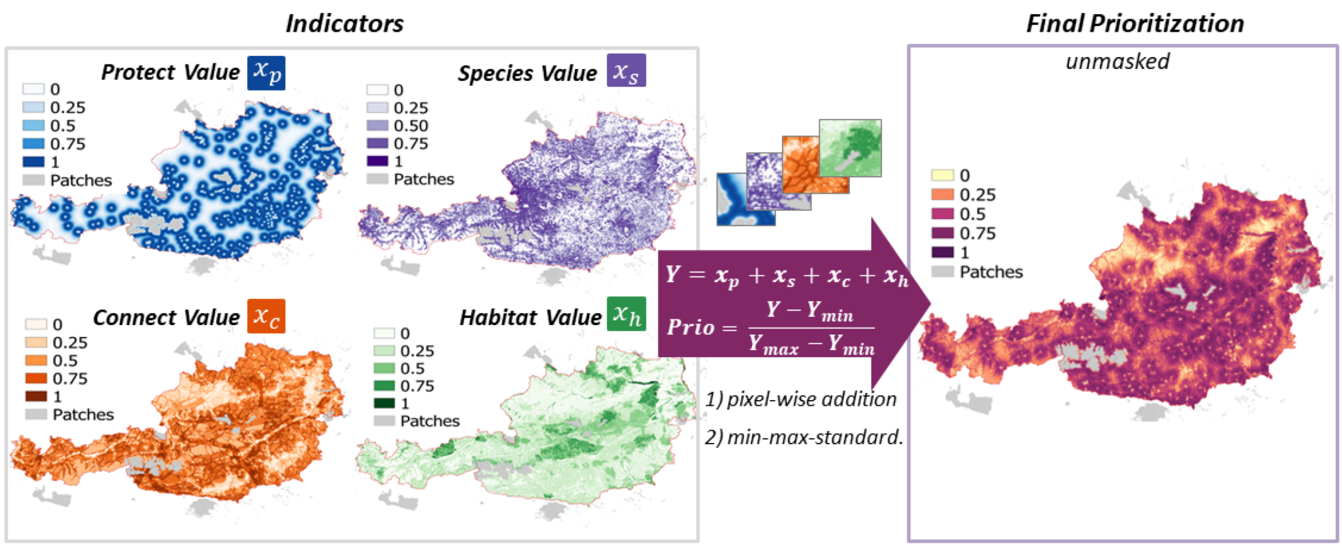

FIGURE 1 Output scheme for the four indicators forming the prioritization value: (i) Protect Value (blue) (ii), Connect (orange) Value, (iii) Species Value (purple), and (iv) Habitat Value (green). The prioritization is calculated by a pixel-wise addition of the four indicators with equal weights. The final prioritization is then standardized by a min-max standardization.

declining pattern with growing distances (see Appendix 2). As the distance distribution curve between protected areas follows a right-skewed (positive) pattern, the indicator is adapted and normalized accordingly. When placing a steppingstone between the protected areas, the distances are halved. Hence, distances around 3 km are set to represent the maximum indicator value of 1—derived from half of the mean distances of 6 km between all protected areas. Distances over 16 km are rated as the minimum indicator value of 0—derived from half of the maximum distance of 32 km between all protected areas.

To identify areas of high connectivity importance, we calculated the *Connect Value*. For this, we included datasets on habitat corridors, Ecological Macro Corridors, Connectivity Areas, and Ecological Intervention Areas, as well as fragmentation (see Appendix 3). These datasets were combined into two sub-indicators: "corridor" and "fragmentation."

The habitat corridors, Ecological Macro Corridors, and Connectivity Areas were combined into a single sub-indicator for "corridor." We created a spatial buffer around the macro corridors and ecological corridors. They were subsequently combined with the connectivity areas by pixel-wise addition of the areas and reclassification of the values according to the overlay intensity (Appendix 3). Furthermore, Ecological Intervention Areas were included to highlight areas where the potential for nature protection, planning, and specific ad-hoc measures to enhance connectivity is high. They were identified in a large-scale project (ALPBIONET2030) analyzing the connectivity potential of the Alpine space and represent regions with high potential for enhancing connectivity and lowering fragmentation through feasible intervention measures. Datasets on habitat corridors in Austria were retrieved from a model created by the Environment Agency Austria (UBA, 2018b). It identifies local ecological wildlife corridors in Austria based on a spatial analysis connecting forest patches within a landscape resistance model and a subsequent expert validation. Datasets on Ecological Macro Corridors, Connectivity Areas, Ecological Intervention Areas, and fragmentation were provided by the Swiss National Park (SNP), ALPARC, and ASTERS, elaborated within the ALPBIONET2030 project (SNP, 2019a, 2019b). Ecological Macro Corridors reveal regions of potential long-distance movement within the European Alpine region; Connectivity Areas point out regions with high priority for action considering the existing landscape barriers and bottlenecks to ensure ecological connectivity between neighboring mountain massifs and the Alps.

We adapted a sub-indicator for "fragmentation" from a fragmentation measure (Lüthi et al., 2019b), that calculates the effective mesh density (number of meshes per 1000 km^2) in the Alpine region. Here, meshes were identified using line data of railroads, roads, and highways as fragmenting structures. The dataset was classified according to mesh density values and favorability to an ecological continuum: Low mesh density translates to a high continuity value and vice versa. In this study, we prioritized areas in which fragmentation is still low and stepping stones can thus help most effectively to protect an ecological continuum.

The *Habitat Value* combines multiple datasets that identify biotopes of high ecological value, key biodiversity areas, and areas of favorable protection status into a single dataset for Austria (see Appendix 4). The dataset includes the national floodplain inventory (UBA, 2011) as well as high-value biotopes of each of the nine Austrian provinces separately (Land Kärnten, 2018; Land Niederösterreich, 2015; Land Oberösterreich, 2021; Land Salzburg, 2022; Land Steiermark, 2007a; Land Steiermark, 2007b; Land Tirol, 2007, 2022; Land Vorarlberg, 2009; Naturschutzbund Burgenland, 2020; Stadt Wien, 2012; Steiermark, 2021), key biodiversity areas derived from a European dataset (BirdLife International, 2021), areas of environmental protection (Lüthi et al., 2019a), and areas of environmental exclusion according to the EUNIS level 3 classification for Austria (UBA, 2018a). The *Habitat Value* does not focus on a certain type of habitat or forest but rather any habitats identified as species-rich, natural, protected, or endangered. Areas are valued regarding their priority for being set aside from management as stepping stone.

To identify species-rich areas, we calculated the *Species Value* (see Appendix 5) by combining nine spatially explicit occurrence point datasets into three sub-indicators: "species richness," "endangered species," and "endemic species." The datasets are retrieved from of point datasets of species observations from the GBIF database. The sub-indicator "species richness" was calculated as the Margalef's Index of species richness (Fedor & Zvaríková, 2018) for each of the seven-point datasets of the kingdoms Plantae and Fungi as well as the classes Reptilia, Amphibia, Mammalia, Aves, and Insecta (GBIF.org, 2022a; GBIF.org, 2022b; GBIF.org, 2022c; GBIF.org, 2022d; GBIF.org, 2022e; GBIF.org, 2022f; GBIF.org, 2022g; GBIF.org, 2022h). The Margalef index is shown in the following formula:

$$D = \frac{S-1}{lnN}$$

with S being the number of different species and N being the total number of all specimens for each grid cell.

Due to highly varying occurrence counts between species groups and in order to make them combinable, each species group's richness was standardized via min-max standardization before being combined into the "species richness" sub-indicator. Subsequently, the "species richness" was log-transformed to achieve a more normalized distribution. The "endangered species" sub-indicator includes an occurrence point dataset of vulnerable, endangered, and critically endangered species as listed by the IUCN (GBIF.org, 2022c). The "endemic species" sub-indicator uses an occurrence point dataset of endemic species (Biodiversity-Atlas Austria, 2022; Rabitsch & Essl, 2009). The sub-indicators "endangered species" and "endemic species" were rated with values of 0 or 1 for absence or presence of these species within each 1.5×1.5 km grid cell. For each occurrence dataset, points within a forest mask (with a 50 m buffer) were filtered and summarized in 1.5×1.5 km grid cells. Finally, all three sub-indicators (species richness, endangered and endemic occurrence) were combined by pixel-wise non-weighted addition and min-max standardization to produce the *Species Value*. The relative contribution of the different groups to the *Species Value* was assessed by conducting a dominance analysis and the results expressed as R^2 values (see Appendix 6). The results indicate that plants (25%), insects (17%), and birds (13%) were the main contributors. This indicates that long distances species, such as mammals (1%) did not bias the result.

It is important to note, that the use of citizen science data bears some limitations as it is not assessed in a systematic and standardized way and therefore it is typically prone to observational bias. Some regions (and species observed) might be better covered than others. Consequently, we present the spatial coverage of the different species groups, endangered and endemic species as well as the standard deviation for different regions in Austria in Appendix 7.

All four indicators were subsequently combined by pixel-wise addition into the prioritization value, rescaled by a min-max standardization and equally weighted (see Appendix 8). To test for potential high sensitivity toward changes in one indicator value, a sensitivity analysis was conducted for the final prioritization. In doing so, four models were chosen with changed weights of one indicator each. Equal weights were kept as baseline model (see Appendices 9 and 10).The standard deviation across models peaks in some regions but stays below a standard deviation of 0.11 across models (see Appendix 11 for all weighted models).

In the final step, we masked the prioritization value to only the forested areas using a high-resolution map of forest cover (1 m × 1 m) for Austria (BFW, 2020) and limiting it to only forest areas that can be taken out of management, excluding areas with protective function (BML, 2022). These areas were excluded because, pursuant to the Austrian Forest Act (ForstG §21), they serve to protect humans, settlements, or infrastructure facilities from natural hazards and must be managed in such a way as to maintain this function. The data were then downscaled to a spatial resolution of 20 m.

2.3 | Data analysis

Each indicator included in the prioritization value was obtained using analysis with QGIS Version 3.16 with integrated PyQGIS, and Pearson correlation analysis was conducted using the R environment version 4.1.0 (R Core Team, 2021) with R package *rstatix* (Kassambara, 2020). A dominance analysis from the "domir" package was run to determine the relative dominance of each species group for Species Value and of each indicator value for final prioritization (Luchman, 2021). We examined the differences in prioritization value among areas of the Austrian *Forest Ecoregions* and *Altitudinal Zones*, and we explored the correlation with landscape parameters like *Distance to Linear Infrastructure*, *Forest Edge Distance*, and *Forest Edge Density* (FED) of the forest areas.

To test whether there were statistically significant differences between *Ecoregions* and respectively *Altitudinal Zones*, we have performed a Kruskal–Wallis analysis with a post hoc Dunn's non-parametric all-pairs comparison test with Bonferroni correction (Kruskal & Wallis, 1952). The Austrian *Forest Ecoregions* (Kilian et al., 1994) are large-scale forest landscapes with largely uniform climatic character and uniform geomorphological units. Austria is divided into 9 main and 22 subregions according to forest ecology aspects, regional climate, and soil conditions A detailed description of Forest Ecoregions in Austria is provided in Appendix 12. *Altitudinal Zones* are climatic and vegetation belts distinguished within each ecoregion. The classification of *Altitudinal Zones* in Austria ranges from colline and sub-montane at lower altitudes to lower montane, montane, and upper montane at medium altitudes and lower subalpine and subalpine at high altitudes. Each of the seven zones is classified by elevation limits depending on local site conditions and plant-sociological aspects. The elevation boundaries for each class vary within each sub-ecoregion (Kilian et al., 1994, p. 12). The landscape parameter *Distance to Linear Infrastructure* is a derived raster showing the distance of each raster cell to the nearest street or railway. It is calculated based on a filtered and merged subset of the OpenStreepMap dataset (OSM) of motorways and railways in Austria (OSM, 2022). We calculated the distance to the nearest line structure using the QGIS proximity tool to obtain Euclidean distances.

Forest edge is defined here as the interface between forest and non-forested ecosystems. The *Forest Edge*

Distance parameter was likewise assessed with the QGIS proximity tool using the outlines (edges) of the high-resolution map of forest cover for Austria (BFW, 2020). As another parameter, we also calculated *FED*. The formula is shown in the following:

$$FED = \frac{L * 10\,000}{A}$$

FED quantifies the intensity of edge effects, showing the relation of forest perimeter length (L) to the corresponding forest area (A) for each forest patch. Low FED values are characteristic for large forest areas and a circular shape; high values are typical for smaller areas with more complex shapes and hence greater edge effects.

3 | RESULTS

We assessed the whole forested area of Austria (39,587 km^2) in order to prioritize areas as stepping stones for biodiversity and forest conservation. The prioritization mask includes 84% (33,344 km^2) of the forest area as generally suitable for stepping stone selection. Then, 16% (6243 km^2) of the forest area is excluded due to either protective function or an already high protection status (Figure 2). Our results show a normal distribution pattern with a mean prioritization value of the total assessed forest area of 0.54 (SD 0.14), a minimum value of 0 and a maximum value of 1. The 75th percentile lies at a prioritization value above 0.64. This means, we detected prioritization values higher than 0.64 in 8336 km^2 (25%) of the assessed forest area. Medium prioritization values (between the 25th and the 75th percentile) range from 0.46 to 0.64 with a median of 0.55. These medium values represent 16,672 km^2 (50%) of the forest area. The 25th percentile is represented by values below 0.46 (Figure 3).

3.1 | Indicator values

All indicator values range from 0 to 1. Except for the *Habitat Value*, all indicators show a normal distribution range. Analysis of the relative dominance of each predictor showed that the *Species Value* was the most important indicator for prioritization (35%), *Protect Value* followed with 33% while *Connect Value* (18%), and *Habitat Value* (13%) were of rather medium importance (Appendix 9).

The *Protect Value* had the highest mean value of all indicators at 0.71 (SD 0.32). The actual mean distance to patches was 6.08 km (SD 4.35 km), with maximum

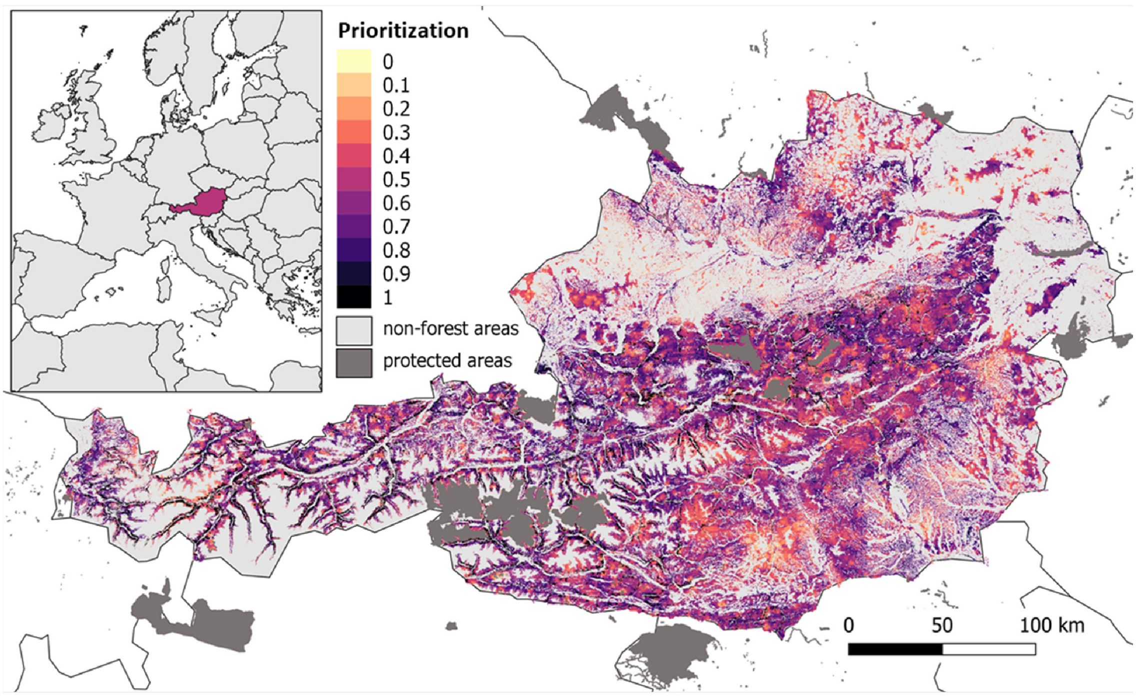

FIGURE 2 Map showing the result of the priority analysis. The values are scaled between 0 and 1 and rate the priority of forest areas (0—low priority, 1—high priority) in Austria for the implementation of stepping stones. The prioritization value is masked using a high-resolution map of forest cover of Austria (BFW, 2020) as base; non-forest areas, areas with a protective function of the forest (BML, 2022), strictly protected areas and highly artificial plantations are subsequently excluded from the prioritization (see Appendix 1 for more details).

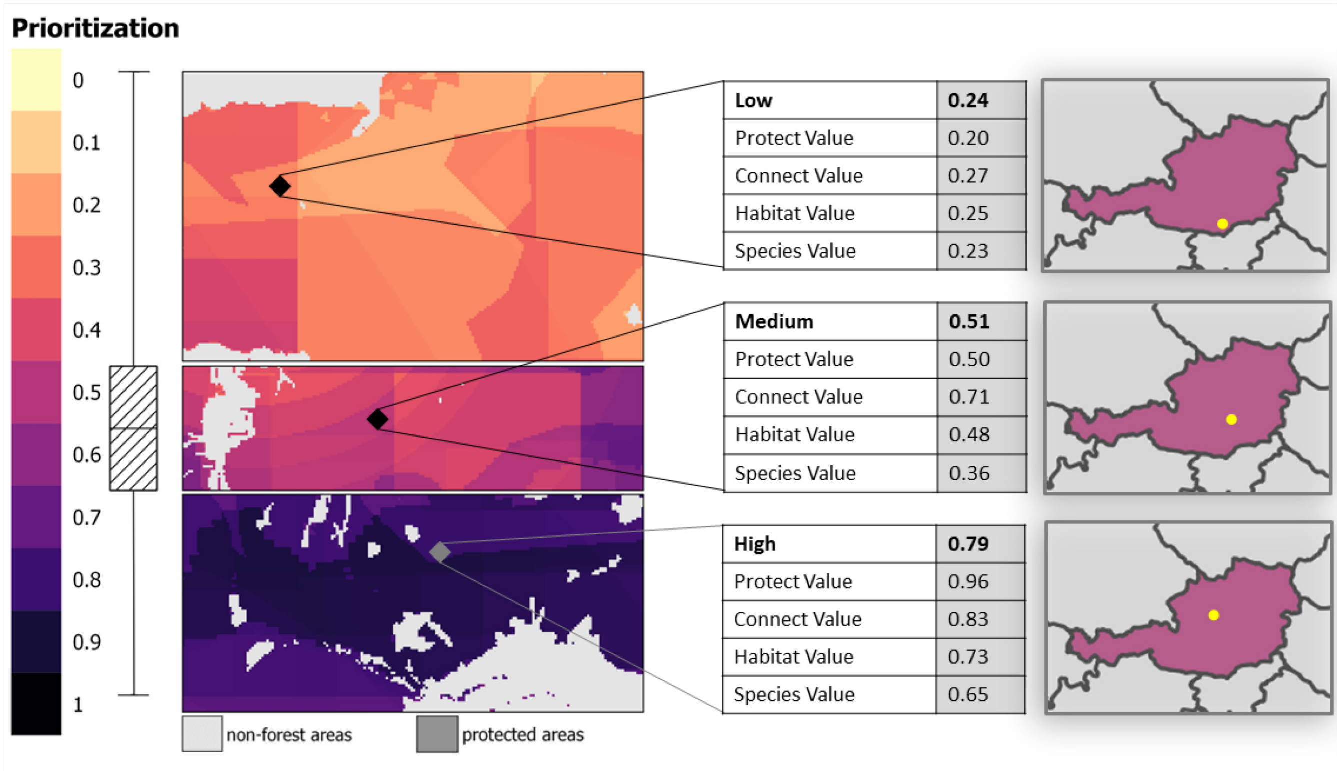

FIGURE 3 Exemplary excerpts of low (<25% quantile), medium (25–75% quantile), and high (>75% quantile) prioritization values distributed over Austria; including the respective values of each indicator separately (protect value, connect value, habitat value and species value). Medium values between 0.46 and 0.64 represent 50% (16,672 km^2) of the forested areas. The schematic maps on the right show the localization within Austria.

distances up to 30.6 km within the assessed forested area. The lowest values of the indicator were found in ecoregions 7.1 Northern Alpine Piedmont—Western Part (mean 0.55, SD 0.37) and 5.2 Bucklige Welt (mean 0.58, SD 0.33), while the highest were found in ecoregions 6.1 Southern Peripheral Region of the Alps—South Margin Part and 5.3 Eastern Peripheral Region of the Alps—East and Central Styrian Part (both mean 0.82, both SD 0.25). Generally, the ecoregions with the highest values showed the lowest standard deviations and vice versa. The differences were significant with a p-value of <.01 (Kruskal–Wallis test, $p < .01$; $\chi^2 = 41{,}408$; df $= 21$). Regarding altitudes, the *Protect Value* was lowest in the colline zone (mean 0.62, SD 0.34) and highest in the montane zone (mean 0.72, SD 0.31).

The mean *Connect Value* was 0.62 (SD 0.22). The highest values were found in ecoregions 5.4 Eastern Peripheral Region of the Alps—West Styrian Part (mean 0.74, SD 0.18) and 6.1 Southern Peripheral Region of the Alps—South Margin Part (mean 0.74, SD 9.17). The three lowest values were found in ecoregions of the Northern Alpine Piedmont, namely in 7.2—West Part (mean 3.5, SD 0.24), and 7.1—East Part (mean 3.6, SD 0.17), as well as in ecoregion 6.2 Klagenfurt Basin (mean 3.7, SD 0.24). In terms of altitudinal zones, the *Connect Value* reached its peak values in the montane and upper montane zones (mean 0.7, SD 0.19), decreasing at higher altitudes (subalpine zone: mean 0.55, SD 0.2) and lower altitudes (colline zone: mean 0.52, SD 0.23).

The *Habitat Value* has the lowest mean of all indicators at 0.34 (SD 0.18) and exhibited a strong singular maximum in ecoregion 5.1 Thermenalpen (mean 0.56, SD 0.18) as well as several low values in regions 1.1 Inner Region of the Alps—Continental Core Zone (mean 0.24, SD 0.13) and 3.3 Southern Transitional Region of the Alps (0.25, SD 0.08). The highest values were found in the colline zone (mean 0.42, SD 0.27) and the lowest in the subalpine zone (mean 0.30, SD 0.23), similarly diminishing with increasing altitudes.

The *Species Value* shows a mean value of 0.36 (SD 0.32). The highest mean values were calculated for the ecoregions 4.1 Northern Peripheral Region of the Alps—West Part (mean 0.53, SD 0.29) and 5.1 Thermenalpen (mean 0.53, SD 0.26), while the lowest were found in 3.1 Eastern Transitional Region of the Alps—North Part (mean 0.16, SD 0.21) and 3.2—South Part (mean 0.18, SD 0.23). Less pronounced (but significant) differences were observed among altitudinal zones (Kruskal–Wallis test, $p < .01$; $\chi^2 = 45{,}027$; df $= 6$). The *Species Value* peaked in the submontane zone (mean 0.42, SD

0.27) and diminished gradually with higher altitudes (subalpine zone: mean 0.3, SD 0.29). The relative dominance of the species groups plants (34%), insects (23%), birds (18%), and fungi (12%) showed the highest contributions to the overall species value (Appendix 6).

3.2 | Differences in prioritization value among ecoregions and altitudinal zones

Nonparametric tests revealed significant differences for the overall prioritization value among ecoregions (Kruskal–Wallis test, $p < .01$; $\chi^2 = 41{,}408$; df $= 21$) (Figure 4). The highest priority for stepping stones was found in ecoregion 5.1 (Eastern Peripheral Region of the Alps) with an average of 0.65 (SD 0.11). Ecoregions 2.2 (Northern Transitional Region of the Alps—West Part) and 4.1 (Northern Peripheral Region of the Alps—West Part) follow closely with mean values around 0.59. By far the lowest values were found in the Northern Alpine Piedmont ecoregions 7.1 West Part (mean 0.44, SD 0.16) and 7.2 East Part (mean 0.44, SD 0.17).

Similarly, we found differences concerning prioritization value among altitudinal zones, as shown in Figure 5. While the median values of the prioritization are visually closely distributed around the mean value of 0.54 (gray dotted line), the differences between the classes are highly significant (Kruskal–Wallis test, $p < .01$; $\chi^2 = 7966$; df $= 6$), with montane regions showing the highest prioritization values (mean 0.57, SD: 0.12), while colline (mean 0.52, SD 0.17) and subalpine regions (mean 0.52, SD 0.14) exhibit the lowest values.

3.3 | Influence of edge distance, edge density, and distance to the nearest road

The analysis of the distance and density of elements potentially altering habitat value (distance to roads,

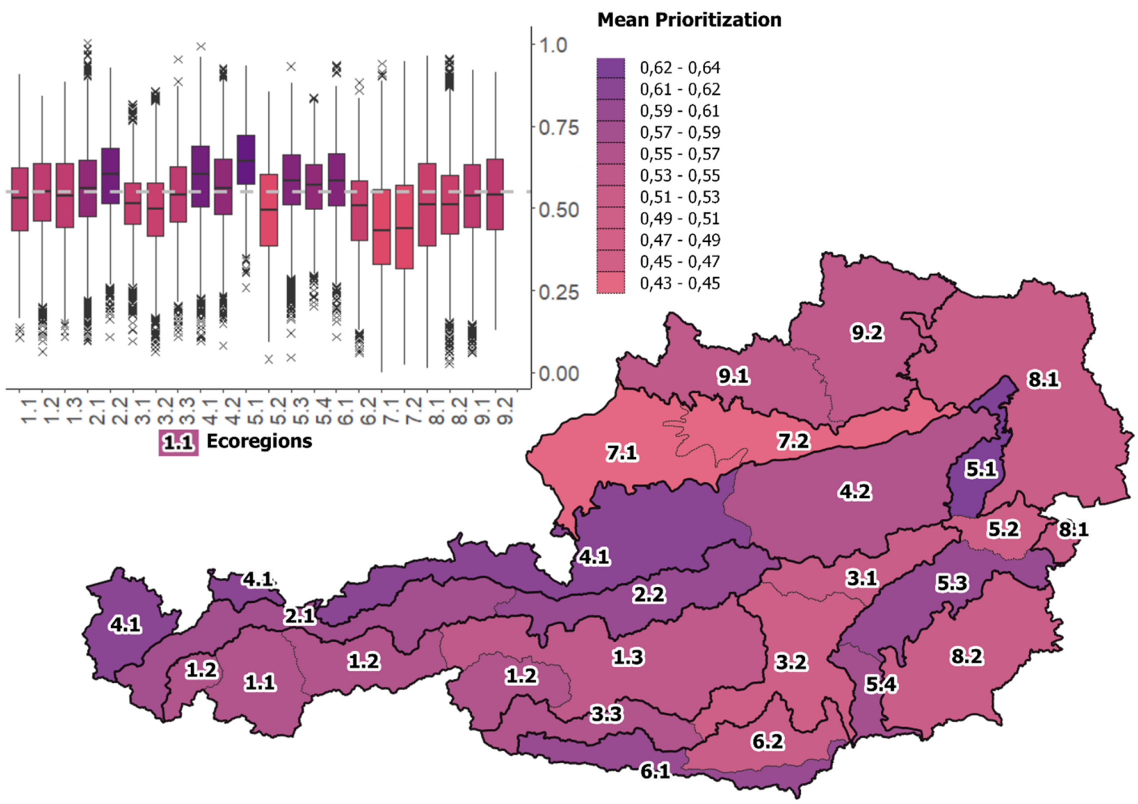

FIGURE 4 Map displaying prioritization value in a color gradient by ecoregion (in numbers 1.1–9.2), showing significant differences among ecoregions (Kruskal–Wallis test, $p < .01$) as well as boxplots showing the value distribution and mean prioritization value for each sub-ecoregion (a detailed description and names of eco-regions is provided in Appendix 11); (1 Inner Region of the Alps with 1.1 Continental Core Zone, 1.2 Subcontinental West Part, 1.3 Subcontinental East Part. 2 Northern Transitional Region of the Alps with 2.1 West Part, 2.2 East Part. 3 Eastern Transitional Region of the Alps with 3.1 North Part, 3.2 South Part, 3.3 Southern Transitional Region of the Alps. 4 Northern Peripheral Region of the Alps with 4.1 West Part, 4.2 East Part. 5 Eastern Peripheral Region of the Alps with 5.1 Thermenalpen, 5.2 Bucklige Welt, 5.3 East and Central Styrian Part, 5.4 West Styrian Part. 6 Southern Peripheral Region of the Alps with 6.1 South Margin Part, 6.2 Klagenfurt Basin. 7 Northern Alpine Piedmont with 7.1 West Part, 7.2 East Part. 8 Eastern Lowlands with 8.1 Pannonian Lowlands and Hills, 8.2 Sub-Illyrian Hills and Terraces. 9 Bohemian Massif with 9.1 Mühlviertel, 9.2 Waldviertel.)

distance to forest edges; FED) showed decreasing prioritization values with increasing distance to the nearest road (Figure 6a), while greater distance to the nearest forest edge led to an increase in prioritization value (Figure 6b). Greater edge density resulted in a lower prioritization value (Figure 6c). Pearson correlation tests revealed significant but weak negative correlations between prioritization value and distance to linear infrastructure ($r = -.008$, $p < .01$), significant but weak positive correlations between prioritization value and distance to the nearest forest edge ($r = .05$, $p < .01$), and likewise significant but weak negative correlation between prioritization and edge density ($r = -.03$, $p < .01$).

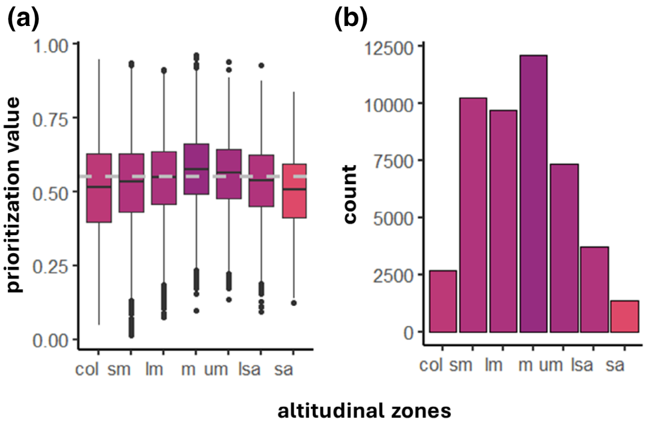

FIGURE 5 (a) Prioritization value by altitudinal zones (x-axis), ordered by increasing elevation (col = colline, sm = submontane, lm = lower montane, m = montane, um = upper montane, lsa = lower subalpine, sa = subalpine). While the median values of the prioritization are visually closely distributed around the mean value of 0.54 (gray dotted line), the differences between the classes are highly significant, with montane zones showing the highest prioritization values (mean: 0.57, sd: 0.12) while colline (mean: 0.52, sd: 0.17) and subalpine (mean: 0.52, sd: 0.14) zones exhibit the lowest values. (b) Value counts by altitudinal zones.

3.4 | Prioritization framework

To enhance the applicability and transferability of the methodological framework of our case study (see Section 2.2), we have developed a generalized prioritization framework (Figure 7). This framework is intended to serve as a facilitator for stepping stone prioritization. It is crucial to adapt the approach to the regional context, target species requirements, and data availability.

To apply the framework effectively, start by collecting data for each value indicator (see Figure 7). Then, calculate the normalized value for each indicator, where 0 represents the least favorable condition and 1 represents the most favorable condition for a stepping stone. For the protection value, adjust the classification based on optimal distances relative to the distribution of focal species or the distance parameters of the study region (refer to Appendix 2). In cases where only basic landscape metrics, such as land cover classes, are available, explicitly calculate wildlife corridors for the study area. Next, create a mask that focuses on the target area of conservation

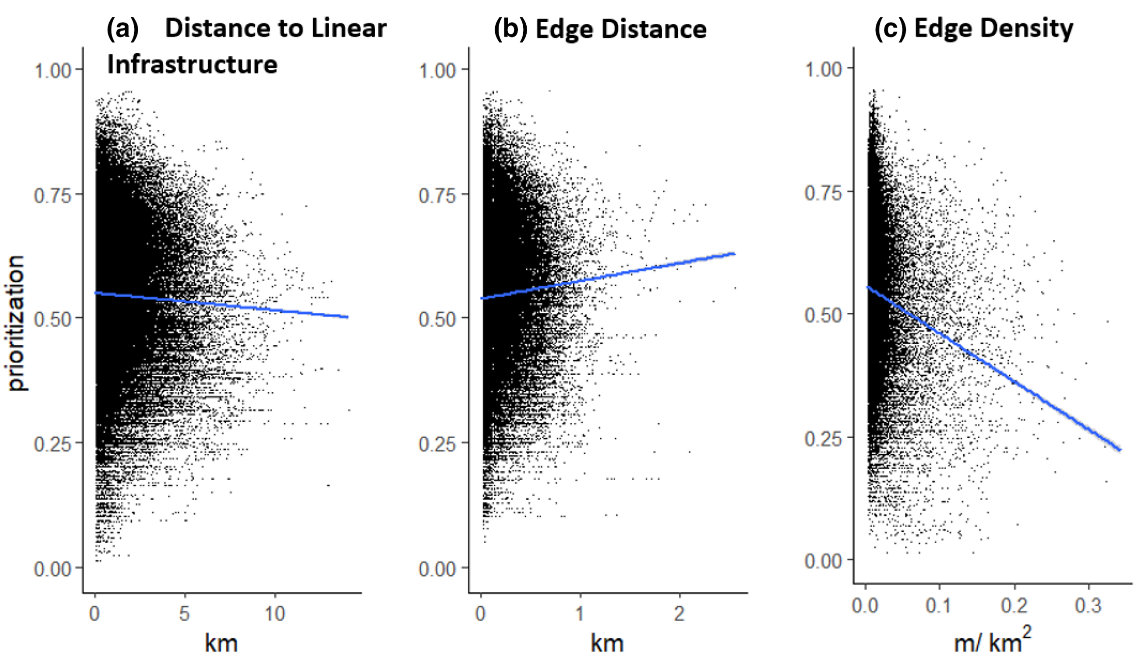

FIGURE 6 Scatterplot of the prioritization value versus (a) distance to linear infrastructure, (b) edge distance, and (c) edge density. Linear regression line (in blue) added to illustrate the effects of distance and edge density on prioritization.

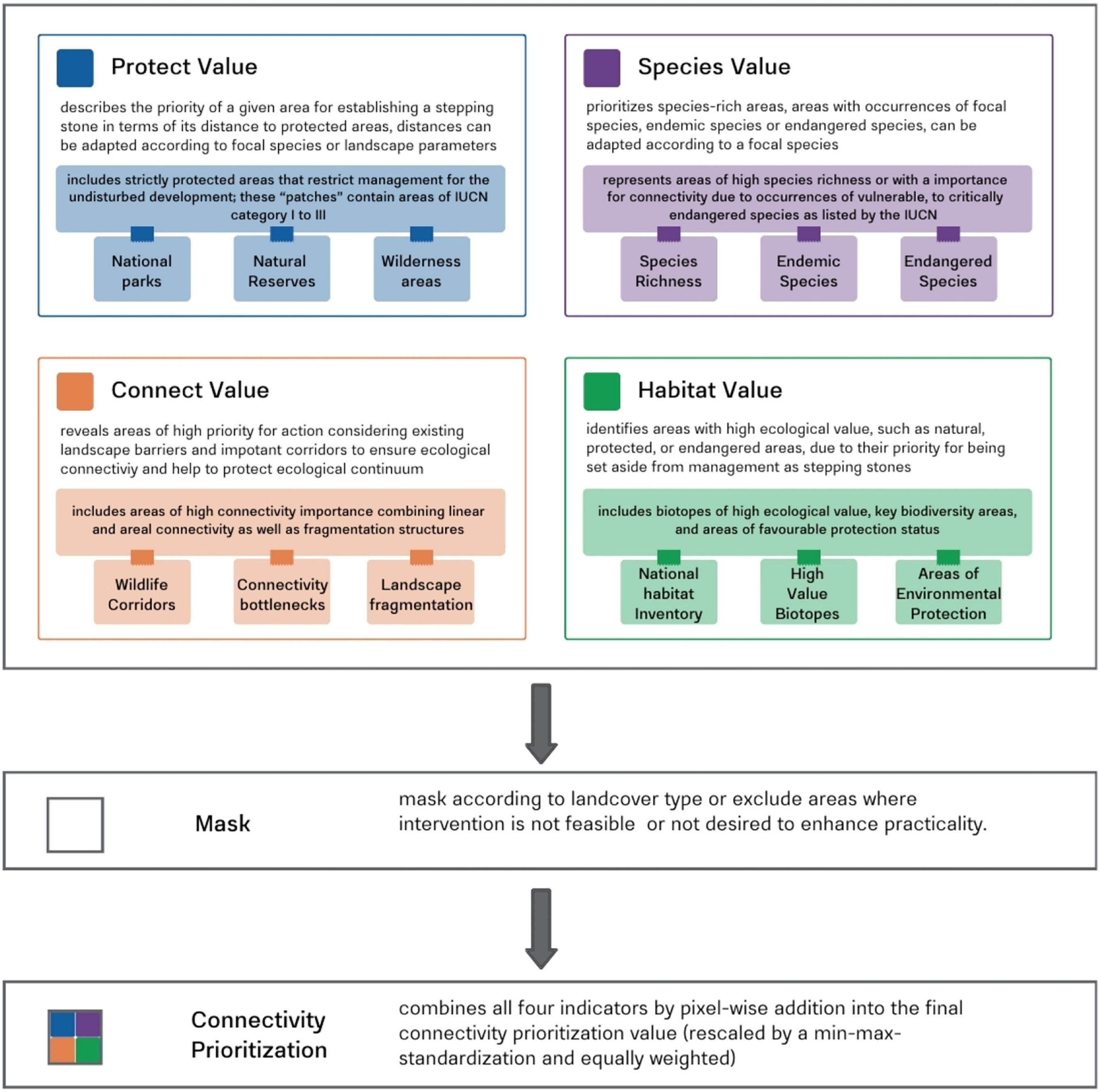

FIGURE 7 Prioritization framework for identifying and prioritizing stepping stones for biodiversity conservation outlines the four prioritization metrics: (i) Protect Value, (ii) Connect Value, (iii) Species Value, and (iv) Habitat Value, as well as the generalized steps involved in applying the approach, guiding users through the process of prioritizing forest areas for biodiversity conservation.

planning, considering factors such as land-use types, specific habitat characteristics, or spatial landscape features. Subsequently, prioritize the calculation by combining pixel-wise addition to generate a prioritization value, which is then rescaled using min-max standardization (Appendix 8). Finally, model validation is essential to understand the distribution of values, assess the influence of each indicator, and identify any potential shortcomings in data selection and combination.

4 | DISCUSSION

Stepping stones are part of most nature conservation strategies in forest ecosystems (Gustafsson, Bauhus, et al., 2020; Lindenmayer & Franklin, 2002; Wintle et al., 2019). The positive effect of this conservation measure has been primarily confirmed in terms of supplying habitats for saproxylic insect species (Gustafsson, Hannerz, et al., 2020; Sverdrup-Thygeson et al., 2014), but also for woodland birds, bryophytes, fungi, and lichen (Kropik et al., 2020; Larrieu et al., 2014; Sverdrup-Thygeson et al., 2014; Wiktander et al., 2001).

Our study provides a novel and spatially explicit framework combining different indicator values of connectivity metrices to prioritize areas for forest biodiversity conservation that are most effective for establishing stepping stones for ecological connectivity (Figure 7). We encourage adapting this framework to local data availability, species requirements, and local conditions. For this study, we conduct dominance analysis of the input indicators as well as correlation analysis of the prioritization with spatial factors. We recommend doing this when applying the framework to understand the behavior of the model.

The presented approach to identification and prioritization is strictly complementary to an assessment of habitat quality and functional connectivity in the field. A limitation of our approach lies in the lack of information on the qualitative habitat characteristics of stepping stones in forests such as tree species diversity, deadwood amounts, or other metrics. Tracking increases in habitat quality of forests for biodiversity. We therefore suggest further research into the precision and reliability of satellite imagery or aerial photography, which could perhaps mitigate this limitation. Several case studies have already shown that the use of high-resolution earth imagery has great potential for nature conservation practice (Guo et al., 2018; Pal et al., 2020; Xia et al., 2018).

We analyze the developed method by revealing the behavior of the prioritization outcome toward the landscape metrics distance to linear infrastructure, edge distance, and edge density, representing spatial distribution of areas and suggesting considerable potential for further connectivity conservation measures. This mainly validates the capacity of the method to identify areas in line with structural ecological considerations. But above all, it increases the understanding of a model with a quite extensive amount of data input and is recommended when applying the framework to a different study area.

The prioritization values increase with increasing distance to forest edges and show a positive correlation with edge density. Both results align with findings that small habitat patches often have lower ecological value than large patches, indicating generally negative ecological effects of habitat fragmentation (Fletcher et al., 2018) and a higher susceptibility to disturbances (Soifer et al., 2021). Following the island biogeography theory (MacArthur & Wilson, 1969), larger patches generally host more species because they provide a greater abundance and diversity of resources, including food and nesting sites (Fernandez-Juricic & Jokimaki, 2001; Zanette, 2000). However, the single large or several small (SLOSS) debate—that is, the question whether a SLOSS reserves represent the superior means of conserving biodiversity in a fragmented habitat—has not yet been satisfactorily resolved, and multiple alternate theories have been proposed since its inception (Arcese & Sinclair, 1997; Calver, 2002; Fahrig et al., 2022; Tjørve, 2010).

Our model results show the tendency of higher prioritization values in close proximity to roads. It is important to acknowledge this model behavior and discuss this outcome resulting from the research aim and selection of input data, which is to identify areas prioritized for the establishment of stepping stones in nature conservation efforts. Transportation infrastructure has been identified as a main pressure causing degradation and fragmentation on ecological connectivity (Clevenger & Wierzchowski, 2006; Strasburg, 2006). Highly frequented roads often represent barriers that affect the behavior of individuals, the genetic diversity of species, and the health of ecosystems through noise, light, and chemical pollution (Mullu, 2016). On the other side, high priority areas near roads require urgent measures to mitigate the negative impacts on their ecological connectivity. Similarly, Liu et al. (2014) conclude that forest stepping stones along critical elements of road networks should be prioritized to sustain their connectivity. To effectively apply the framework for stepping stone prioritization across diverse contexts and regions, we recommend considering all four indicators from the early conservation planning stage. Additionally, we emphasize allocating sufficient time for preliminary planning to secure access to necessary data sources, relevant research projects, and expert knowledge prior to conducting the analysis. Furthermore, Iezzi et al. (2022) argue that the importance of stepping stones identified using forest-patch prioritization mapping tools greatly depends on the target species' dispersal abilities. To overcome this potential bias, we recommend focusing not on few specific target species but rather on a combination of structural and functional indices. Although focusing on keystone, flagship, or umbrella species (Simberloff, 1998) as indicators for forest biodiversity is a valuable conservation strategy (Barua, 2011; Hansson & Angelstam, 1991; Oettel & Lapin, 2020), the applicability of this approach to the assessment of ecological connectivity has been demonstrated by selecting surrogate species (Dutta et al., 2023; Lechner et al., 2017; Meurant et al., 2018).

We identified high priority areas for habitat connectivity in the peripheral and transitional regions of the Alps, and in montane to submontane altitudinal zones and therefore encourage the consideration of stepping stone priority within the local and regional context. The Austrian land surface is characterized by a rich diversity of geomorphological areas resulting in a great variety of ecosystems (Grabherr et al., 2003; Lorenz et al., 2004). In particular, the forest ecosystems are influenced by elevation, geomorphology (Dyderski & Pawlik, 2020), and climatic conditions (Seidl et al., 2017; Thom et al., 2017), as well as by a history of forest management (Johann, 2007).

The connection of forest management and forest ownership is strong, manifesting as a more intensive forest management in small-scale forest ownership and a trend toward more extensive management in public forest ownership (Oettel et al., 2022). In Austria, a substantial 82% of forests are privately owned, the remaining 18% of forests are publicly owned (BFW, 2019). The emphasis on extensive management in publicly owned forests can be attributed to the implementation of integrative nature conservation strategies, with a focus on preserving "old-growth islands" (ÖBf, 2008). These strategies find resonance in other European countries (e.g. Ekbom et al., 2006; Gustafsson et al., 2012; Laarmann et al., 2009). That is why there is an increasing need to establish stepping stones to promote ecological diversity and improve the conservation of forest biodiversity (Da Rocha et al., 2021; Lapin et al., 2019; Pirnat, 2000). For some species such as wood-living beetles, bryophytes, or liverworts (e.g. Djupström et al., 2008; Perhans et al., 2009), the provision of stepping stones can potentially provide a critical habitat quality or type that is lacking in a landscape of managed forests. From a conservation management perspective, a dense spatial occurrence of stepping stones in a forested landscape can be an important complement to traditional protected areas (Perhans et al., 2009). Consequently, it becomes evident that higher conservation efforts are necessary especially in private forests to implement integrative conservation measures, possibly by the retention of single old trees or stepping stones (Oettel & Lapin, 2020). This is especially pertinent in the light of the expected future climate-induced range shift of forest species. The creation of a network of stepping stones, particularly in areas bridging warmer and cooler climates, can significantly support the adaptation of forest species to changing climatic conditions (Han et al., 2021). The development of further tools for spatially explicit identification and prioritization may include assessments of site-specific biodiversity conservation needs that take projections of expected future changes into account.

5 | CONCLUSION

In this study, we demonstrate the utility of spatial analysis of indicator values for conserving ecological connectivity in forest habitats, utilizing a newly proposed framework to identify and prioritize stepping stones. The presented methodological framework is a useful tool to support concise and reasonable spatial decision making on a national scale for the selection of stepping stones. It helps to maintain an overview on necessities and potentials on a large scale. However, the framework requires regular updating of accessible biodiversity-related data and is not a substitute for on-the-ground assessment of habitat quality. We argue that as regional and local monitoring data become more available, areas for conservation actions to improve connectivity can be more accurately identified and prioritized, increasing the effectiveness of conservation measures in the long term.

Assessing a prioritization value for forested landscapes can only be the first step in implementing conservation measures. Further steps to be considered after applying the presented framework include the following: First, consensus and support for establishing stepping stones by private and public forest owners is at least as important for the success of conservation measures as precise analysis of biodiversity data. Second, a biodiversity assessment identifying key indicators of connectivity and forest biodiversity should be undertaken. Third, an active long-term monitoring protocol should be developed to assess trends and influences on the stepping stones. Finally, we recommend considering habitat connectivity in the planning process for new protected areas. The connectivity of forest habitats will be increasingly important under future climate change conditions to facilitate the range shift persistence of forest-dependent species (Han et al., 2021). Protected areas of unmanaged forest provide important habitats for forest-dependent species, but they need to be embedded in a network of corridors and stepping stones allowing species to migrate to more suitable forest areas. Further research and practical knowledge should focus on developing climate-smart management measures for habitat connectivity.

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DATA AVAILABILITY STATEMENT

Data supporting the results of the paper will be archived to the repository of Austrian Research Centre for Forests https://www.bfw.gv.at/en/.

ORCID

Katharina Lapin https://orcid.org/0000-0003-4462-2058
Johanna A. Hoffmann https://orcid.org/0000-0003-1087-8821
Martin Braun https://orcid.org/0000-0001-5364-8140
Janine Oettel https://orcid.org/0000-0002-3037-9563

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SUPPORTING INFORMATION

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

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