

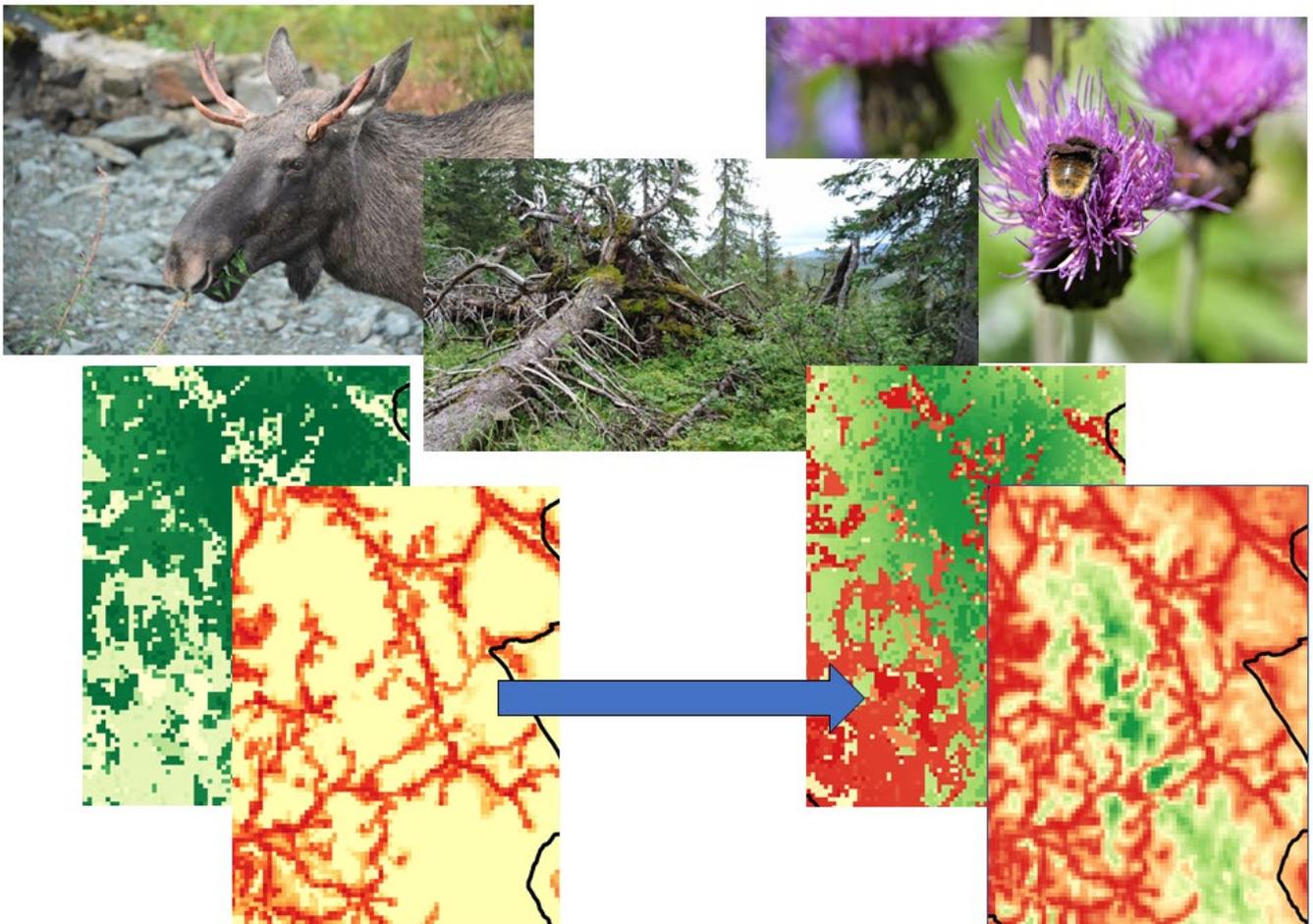
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NINA Report

Modelling green infrastructure for conservation and land planning – a Pilot Study

Suggestions for analyzing the functional connectedness of high-quality habitat to aid sustainable land use planning

Erik E. Stange
Manuela Panzacchi
Bram van Moorter



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Abstract

Stange, E.E., Panzacchi, M. & van Moorter, B. 2019. Modelling green infrastructure for conservation and land planning – a pilot study. NINA Report 1625. Norwegian Institute for Nature Research.

Green infrastructure (GI) are the areas that are crucial for species' ecological processes, defined by the interacting components of habitat quality and connectivity. Land use that maintains GI helps prevent loss of biodiversity and ecosystem services. Researchers and decision makers need analytical tools for identifying GI and assessing the potential impacts of land use and climate change. The Norwegian Environmental Agency sought to explore the potential for developing a GI modelling protocol suitable for assessing GI at the municipal levels using Norwegian-scale data sources. In this report, we present a methodological protocol for identifying GI by building on recent innovations in connectivity studies, movement ecology and computer science.

Connectivity is a function of the species that move within a landscape, and not a property of the landscape itself. Accordingly, we stress the necessity of using a species approach to GI modelling to account for space use patterns determining species' interactions with the landscape. The protocol we present begins by formulating clear goals for ecology and land management. This will drive selection of the appropriate focal species and data to be used, through either analytical modelling or expert opinion, to produce model inputs of habitat quality (where individuals spend most time) and landscape friction (how easy it is to traverse each landscape unit, or pixel). We use the Randomized Shortest Path (RSP) algorithm to identify all possible movement paths between all pairs of pixels in the landscape, and the likelihood of an individual walking through each of them. RSP provides more realistic representations of animal movements than either Least Cost Path or Random Walk-based algorithms. We then use the Probability of Connectivity formula to integrate habitat quality and assess the likelihood that each pixel would be used by the focal species, based upon both its quality and its accessibility from all other areas. The outputs are two complementary metrics that quantify the two interrelated aspects of GI: 1) *Habitat Functionality*, describing the combined connectedness of high-quality habitat for the focal species (the amount of individuals expected to be found in each pixel), and 2) *Movement Flow*, identifying the areas that serve as important connectors (where a larger flow of individuals is expected).

We demonstrate use of this protocol with examples in Ski municipality to illustrate different degrees of model complexity, parameterization approaches (expert-based vs. data driven), and the GI of species with different movement abilities and ecological requirements. The moose model provides an example of an extensively-studied focal species with GPS tracking data used to parameterize habitat quality and landscape friction. The insect model associated with old growth forests is an example of a much simpler approach building upon expert assessments. The model for bumblebees presents a combination of both data-derived parameters and expert knowledge.

The protocol's strong theoretical foundations in ecology and network theory allows us to model the ecological mechanisms underlying loss of functional habitat and to predict how landscape and climatic changes might impact species. This is a major advantage over simpler approaches that have more limited theoretical support and predictive abilities. The modelling protocol has been developed specifically to support long-term connectivity conservation land-planning. Hence, we provide details on how to use GI results to assess cumulative impacts, conduct scenario analyses for assessing consequences of climatic or anthropogenic changes in the landscape and prioritize areas for protection or restoration. This protocol can be applied to a range of species to help inform land use planning at municipal, regional and national scales.

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Norsk sammendrag

Stange, E.E., Panzacchi, M. & van Moorter, B. 2019. Modelling av grøn infrastruktur for bevaring og arealplanlegging – en pilotstudie. NINA Rapport 1625. Norsk institutt for naturforskning.

Grønn infrastruktur (GI) er arealene som er avgjørende for arters økologiske prosesser, med utgangspunktet i samspillet mellom habitatkvalitet og konnektivitet. Arealbruk som opprettholder GI bidrar til å forhindre tap av biologisk mangfold og økosystemtjenester. Forskere og beslutningstakere trenger analytiske verktøy for å identifisere GI og vurdere potensielle konsekvenser av arealbruk og klimaendringer. Miljødirektoratet ønsket å utforske muligheten for å utvikle en modelleringsprotokoll for GI som er egnet for å vurdere GI på kommunalt nivå, men med nasjonalt omfang ved hjelp av nasjonalt dekkende datakilder. I denne rapporten presenterer vi en metodologisk protokoll for å identifisere GI som bygger videre på nyere innovasjon innen tilkoblingsstudier (konnektivitet), bevegelsesøkologi og datavitenskap.

Konnektivitet er en funksjon av artene som beveger seg innenfor et landskap og ikke en egen-skap av landskapet selv. Derfor understreker vi nødvendigheten av å bruke en artsbasert tilnærming til GI-modellering for å redegjøre for bevegelsesmønstre som avgjør artens samspill med landskapet. Protokollen vi presenterer formulerer klare mål for bevaring og arealforvaltning. Dette driver utvalget av aktuelle *fokalarter* for modellen og hvilke data som skal brukes som input i modellen for habitatkvalitet (hvor individer bruker mest tid) og landskapets friksjon til bevegelse (hvor lett det er å krysse hver landskapsenhet eller piksel). Vi bruker algoritmen *Randomized Shortest Path* (RSP) for å identifisere alle mulige bevegelsesbaner mellom alle pikselpar i landskapet, og sannsynligheten for at et individ bruker hver av dem. RSP gir mer realistiske representasjoner av dyrebevegelser enn både *Least Cost Path* eller *Random Walk*-baserte algoritmer. Deretter bruker vi *Probability of Connectivity*-formelen til å integrere habitatkvalitet og vurdere sannsynligheten for at hver piksel vil bli brukt av fokalararten, basert på både kvaliteten og tilgjengeligheten fra alle andre områder. Resultatet er to komplementære beregninger som hver for seg beskriver en av de to sammenhengende aspektene av GI: 1) *Habitat functionality* (habitatfunksjonalitet) som beskriver den kombinert konnektiviteten av høykvalitets habitat for fokalararten (mengden individer forventes å bli funnet i hver piksel), og 2) *Movement Flow* (bevegelsesflyt) som identifiserer områdene som utgjør viktige forbindelser (hvor en større strøm av individer kan forventes).

Vi demonstrerer bruk av denne protokollen med tre eksempler i Ski kommune for å illustrere ulike grader av modellkompleksitet, parametreringsmetoder (ekspert-basert versus data-basert) og GI for arter med forskjellige bevegelsesevner og økologiske krav. Elgmodellen gir et eksempel på en art som er grundig forsket på og hvor vi kan bruke GPS-sporingsdata til å parametere habitatkvalitet og landskapsfriksjon. Modellen for insekter som er forbundet med gamle skoger er et eksempel på en mye enklere tilnærming som bygger på ekspert vurderinger. Modellen for humler presenterer en kombinasjon av både data-basert parametere og ekspertkunnskap.

Protokollens sterke økologiske grunnlag og nettverksteori tillater oss å modellere de økologiske mekanismene som ligger til grunn for tap av funksjonelt habitat og å predikere hvordan landskaps- og klimaendringer kan påvirke artenes forekomster. Dette er en stor fordel mot enklere tilnærminger som har begrenset teoretisk støtte og prediktive evner. Protokollen er utviklet spesielt for å støtte arealplanlegging for langsiktig bevaring av konnektivitet. Derfor beskriver vi hvordan man kan bruke GI-resultater for å vurdere samlede belastning, gjennomføre scenarioanalyser for å vurdere konsekvenser av klimatiske eller menneskeskapt endringer i landskapet og identifisere områder for beskyttelse eller restaurering. Denne protokollen kan brukes på en rekke arter for å bidra til å informere arealplanlegging på kommunale, regionale og nasjonale skalaer.

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Foreword

The Norwegian Environmental Agency issued a call for proposals to develop a methodology for modelling Green Infrastructure (GI) to support decision making and land planning at the municipal level. The conceptual foundation for this work was provided in a report written by Framstad et al. (2018), which outlined relevant criteria for identifying important components of GI in various major ecosystems and identified the relevant data sources for mapping and assessing GI in planning tools.

The report describes the theoretical foundation of modelling GI, and proposes a protocol that can provide valuable insight into species space use patterns and their interactions with a changing landscape. We draw from active areas of research that NINA continues to work within, providing examples of species-based GI models.

We would like to thank Trond Simensen from the Norwegian Environmental Agency for useful information and important feedback through the course of this project. Thanks also to Erik Framstad, who participated in the initial stages of planning this work.

Lillehammer, April 30, 2019

Erik Stange
Project leader

1 Introduction

1.1 Background

Green infrastructure (GI) are the areas and landscape features with important roles for species' life cycles and ecological processes. The GI concept has experienced a growing prominence in conservation and land planning over the past decade because GI is a very useful conceptualization that communicates the important interactions between habitat quality and its connectivity. The GI concept is now the basis for major conservation and sustainable land planning initiatives worldwide. Green infrastructures are a key component within the EU 2020 Biodiversity Strategy (CBD 2010), and its Aichi Target 11 calls for conservation of "ecologically representative and well-connected systems". GI is increasingly visible within Norwegian sustainable land management strategies. For example, the Norwegian Government's action plan for biodiversity calls for investigating the need for a better conservation of ecological connectivity and—importantly—also seeks solutions for how to achieve this goal (Det kongelige Miljøverndepartementet 2015).

Researchers, managers, and land planners understand that sustainable landscape planning requires robust knowledge on how landscape changes simultaneously affect habitat quality and the landscape connectivity required to support species movements—both under present conditions and under future scenarios of changes in climate, land use, and anthropogenic development. We need robust methods to quantify habitat that is simultaneously of good quality and well-connected so that we may properly assess the total, cumulative effects of anthropogenic changes to the environment and find comprehensive solutions in terms of sustainable land planning (de la Fuente et al. 2018, Saura et al. 2018). Analytical methods to assess GI for land use planning must be ecologically sound, applicable to any species or ecosystem, and able to produce maps of GI at a resolution and spatial extent that are appropriate for land planning at regional and local scales. Finally, methods need to be able to assess cumulative impacts under scenarios of environmental changes and form a solid basis to guide the prioritization of areas for long-term conservation.

Developing methodologies to identify GI requires an interdisciplinary effort that involves ecologists who specialize investigating habitat quality, movement ecology and landscape connectivity, as well as mathematicians, data managers, computer scientists, software developers and social scientists who can guide the application of such methodologies in the societal context (see European Commission 2012). The development of integrated methods to identify and assess GI effectively constitutes a new research field that is under active development within the international research community (European Commission 2012).

The goal of this project, as expressed by the Norwegian Environmental Agency (NEA), is to develop a method for geographic modelling of GI in Norway using existing data available at the national scale. The models developed in this project should be capable of identifying important ecological areas and connections within the landscape at a spatial scale that would be relevant for sustainable land use planning down to the municipal level and scalable to larger extents. The impetus for this project stems from a report produced by a committee of experts on Norwegian GI that provided general recommendations for how green infrastructure should be identified and assessed (Framstad et al. 2018).

In this report, we present a methodological protocol for identifying and assessing GI that has been developed through several years of close collaboration within an international and interdisciplinary team. The approach we present builds on several recent innovations in connectivity conservation, movement ecology and computer science. This approach aims to both identify existing GI and provide tools useful for long term connectivity conservation and land planning.

1.2 What are green infrastructures?

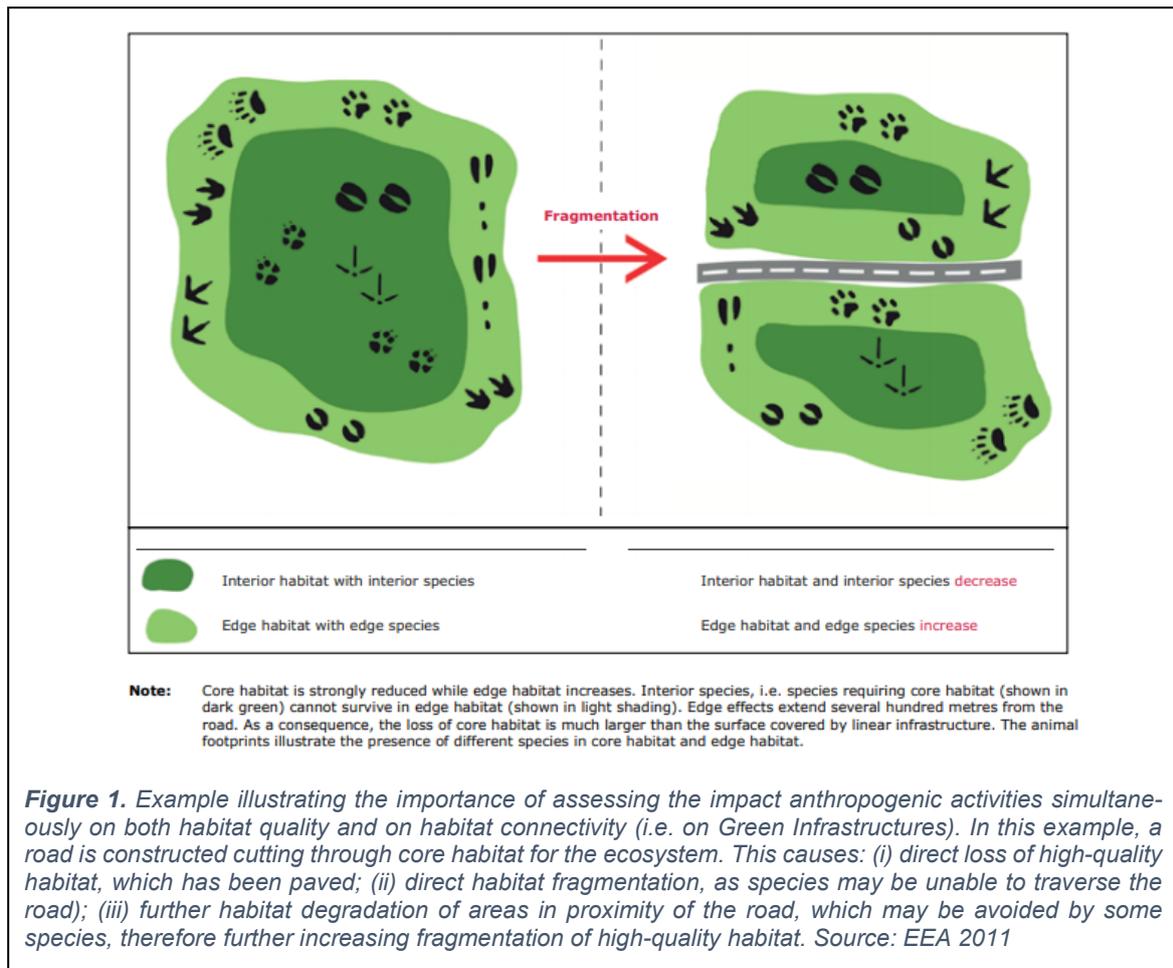
While the Green Infrastructure (GI) term is widely used in national and international policies, it does not have a single, widely-recognised definition. Because of the multifunctional character, GI has been defined in a variety of ways corresponding to a wide range of design-, conservation- and planning-related disciplines that have adopted the concept (see <https://www.interreg-central.eu/Content.Node/Definitions.html> for numerous examples from science and policy). However, most definitions build upon two interacting components: **habitat quality** and **connectivity**. As an example, we provide the European Commission's definition (2013), which is perhaps the most frequently cited:

*“Green Infrastructures are a strategically planned **network of high quality natural and semi-natural areas** with other environmental features, which is designed and managed to deliver a wide range of ecosystem services and protect biodiversity in both rural and urban settings”.*

This definition identifies the twofold goals of both protecting biodiversity and providing ecosystem services. At the requests of the Norwegian Environmental Agency (NEA), and consistent with the approach prescribed by Framstad et al. (2018), our methodological approach primarily addresses assessing GI with respect to biodiversity. Yet because an ecosystem's biodiversity generally defines its capacity to deliver many ecosystem services, the approach we present can also be applied to assess spatial dimensions of any type of ecosystem service. Whether they address biodiversity or the ecosystem services they provide, all GI assessments entail an integration of information regarding species' habitat requirements (i.e., habitat quality) with the properties of species and landscapes that dictate organisms' movements (i.e., corridors and barriers). Together, these two aspects determine the connectedness or connectivity of green infrastructure within the landscape.

1.3 Interactions between habitat loss and fragmentation

Habitat loss and habitat fragmentation constitute the greatest threats to global biodiversity (Brook et al. 2008). Slowing the current rate of biodiversity loss requires understanding of how human activities contribute to habitat loss and fragmentation, and how land management can minimize negative impacts. Researchers have traditionally treated habitat loss and habitat fragmentation as separate phenomena, each belonging a different branch of ecology with their own methodological approaches built upon different theoretical foundations. However, we now see an emerging realization that *habitat loss and fragmentation are highly interdependent*. For example, when a motorway crosses an area of suitable habitat for species or ecological communities, it may create fragmentation by impeding movements of individuals and thus restrict their access to important trophic or genetic resources (**Figure 1**). Yet a new motorway will also lead to habitat loss due to both degradation of the area where the road lies and reduction of the habitat's core if species avoid the habitat periphery (i.e., the areas near the road). Climate changes will only exacerbate effects of fragmentation and habitat loss. Species may not be able to access areas with more favourable climatic conditions if old and new habitat areas are not sufficiently connected (Opdam & Wascher 2004). If we ignore this interaction between habitat loss and fragmentation, or the cumulative effect they have, it may lead to an incorrect prioritization of areas for conservation and restoration.



1.4 Structural versus functional connectivity

Landscape connectivity addresses the “degree to which the landscape facilitates or impedes movement among resource patches.” (Taylor et al. 1993). It also addresses the “functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure” (With 1997). The types, amounts, and spatial arrangement of landscape features influence both the organisms’ movement and the ecological functions generated through such movements. The connectivity of suitable habitat determines both species’ population dynamics and ultimately the structure of entire ecological communities. The study of landscape connectivity aims at **linking the physical structure of the landscape with an organism’s response to that structure** (Taylor et al. 2006).

Assessing structural connectivity is far simpler than assessing functional connectivity, both methodologically and in terms of data requirements and computational power. This explains the predominance of structural connectivity analyses in the early connectivity literature. The assumption inherent in structural connectivity analyses is that contiguous habitat patches support species’ movements through them. However, this approach ignores the actual movement behaviour, motivations and space use patterns of organisms that may—or may not—interact with these patches. Unfortunately, the relative simplicity of structural connectivity analyses has resulted in the **misperception that connectivity can be a property of the landscape, rather than of the species interacting with it** (European Commission 2012).

Hundreds of studies derive metrics of connectivity that describes the spatial linkages among patches defined by various anthropocentric habitat categories (e.g. forest, wetlands, meadows,

etc.). However, the assumptions inherent in this approach have numerous important flaws. A given habitat category will have different connectedness for different organisms depending on species' dispersal modes, capacities and behaviours. Patches can also be structurally connected but still functionally isolated if they do not support the necessary ecological processes. Similarly, patches that are structurally isolated can still be functionally connected if individuals are capable of crossing areas of poor-quality habitat (Tischendorf & Fahrig 2003, With 1997). Perhaps most importantly, the structural connectivity approach does not allow to draw any conclusions regarding the contribution of the landscape to support an ecological function of interest (e.g. dispersal, migration, metapopulation dynamics).

Functional connectivity, on the other hand, incorporates species' behaviour and ecological processes to describe the mechanisms driving species' space use patterns and their interaction with different landscape. For example, functional connectivity might refer to the identification of landscape elements that support animal migration in a specific area. Such landscape elements may or may not be contiguous (e.g. migration can take place also through "stepping stones") and may or may not represent optimal habitat for the species (e.g., migrating individuals frequently traverse areas without adequate trophic resources on route to a target range). Hence, the concept of functional connectivity represents the *actual landscape connectivity from the species' perspective and is therefore far more appropriate for identifying and assessing Green Infrastructures*. While the vast majority of analyses describe landscapes' functional connectivity for animal species, the principles apply to species of all life forms.

1.5 Connectivity for multiple species: can one size fit all?

Simplistic metrics describing only structural connectivity may generally be too crude to be ecologically relevant. In the case of rare or endangered species or species of special interest, it is crucial to use the most robust species-specific approaches available to identify functional connectivity. Of course landscape-level planning assessments generally need to address the needs of the broader biodiversity and do not have infinite resources that would be necessary for evaluating the functional connectivity for all species present in a landscape. So connectivity metrics must be pragmatic and based on attainable data that can reduce the many dimensions of multiple species requirements to a manageable set of criteria (Wiens et al. 2008). *Surrogate species* can be used as proxies for broader sets of species when the number of species of conservation concern is too high. A frequently used approach involves identifying an "umbrella" species as a surrogate. Umbrella species are commonly used to reduce the complexity of quantifying biodiversity for conservation purposes, since the presence of an umbrella species indicates high taxonomic diversity (Sattler et al. 2014), and umbrella species' protection would indirectly protect other co-occurring species. Umbrella species used in connectivity analyses generally have broad home ranges with habitat requirements and movements that represent or encapsulate an important proportion of an area's native species and ecological processes (Breckheimer et al. 2014), such that their protection would indirectly protect other species dwelling there.

There may be shortcomings to basing connectivity assessments on a single species (Siddig et al. 2016), even if that species might possess qualities of an umbrella species. One size does not fit all. Strategies designed to meet the needs of umbrella species cannot ensure the conservation of all co-occurring species because some species are inevitably limited by ecological factors that are not relevant to the umbrella species (Roberge & Angelstam 2004). Instead, connectivity conservation should focus on an array of native species—as implied in the definition of green infrastructure. The term *surrogate species* refers to species whose habitat preferences and movement patterns are representative of a portion of the biodiversity, including species that do not have qualities of umbrella species.

Evidence of overlap in dispersal habitat of several surrogate species can provide the basis for connectivity assessments, although the most suitable surrogate species may not be the most intuitive. Breckheimer et al. (2014) provide an example of using three threatened species—a bird

(the umbrella species), a butterfly and a frog—that inhabited the same fragmented landscape. Despite considerable differences in the species' ecologies, the three species had substantial overlap in the areas that were important for their dispersal. While the bird, as a presumed umbrella species, was perhaps the more intuitive surrogate, it did not have the highest overlap with other species in terms of which areas supported connectivity. Wang et al. (2018) investigated how well connectivity corridor planning based on the iconic giant panda *Ailuropoda melanoleuca* preserved suitable habitat and its connectivity for other focal species. They found that a multi-species approach was better at identifying priority areas for corridor conservation that maximized benefits to both pandas and a broader suite of mammals. Decision-makers should recognize the limitations of using any single species, if the aim is to preserve general biodiversity (Sattler et al. 2014).

Another option for a GI model surrogate involves identifying a *dispersal guild*, or a group of organisms that have similar fine-scale movement behaviour (Lechner et al. 2017). Dispersal guilds resemble ecological guilds and are traditionally defined as “a group of species whose members exploit similar resources in a similar manner” (Park & Allaby 2013). However, dispersal guilds expand the definition of ecological guilds to also include species' dispersal characteristics. Species within a dispersal guild will therefore have both similar habitat preferences and requirements and a similar capacity for movement within and among areas of suitable habitat. This approach represents an intermediate between single species models and habitat-based analyses of structural connectivity because it bases a GI model in explicit ecological attributes of an identifiable subset of organisms without the data requirements that many single species models have. When available, information on single species can be aggregated into common groups and provide greater generalizability of the results.

Again, one size does not fit all, nor is there a single recipe describing which focal species will be best suited for GI models that can support sustainable land planning for general biodiversity. GI models can focus on a single species of interest to address a specific management issue (e.g., to reduce wildlife collisions with automobiles), on an umbrella species representing the habitat requirement of several local species, or on a selected array of species with different habitat requirements. This decision of which species or species groups to use should be based upon a well-informed discussion regarding the aim of the project (“Green Infrastructure for what?”), involving all those that could provide relevant knowledge for the area of interest.

1.6 Selecting surrogate species for GI modelling

We stress the importance of using species-based models for generating ecologically realistic assessments of GI, which can generate verifiable predictions of how landscape connectivity will affect species conservation. Municipal land planners will likely find that GI models based on appropriate surrogate species are also highly effective for engaging discussion with local stakeholders because the models are targeted towards species-specific habitat requirements and based on explicitly-defined ecological processes (Wiens et al. 2008). As we discussed above, it is unrealistic to expect that the movement requirements for any one species will adequately represent those of all other species of conservation concern, even within groups of species that share common habitat requirements. Designing GI assessments that involve multiple surrogate species will therefore be a better approach with more generalizable results than assessments that employ only a single surrogate species. GI assessments for land use planning in Norwegian municipalities will obviously not have unlimited resources for GI models of large numbers of surrogate species. Fortunately, several studies provide empirical support that connectivity analyses that include a manageable number of systematically selected surrogate species can adequately and accurately reflect the movement needs of broader species assemblages (Cushman et al. 2013, Krosby et al. 2015, Meurant et al. 2018, Opdam et al. 2008, Roberge & Angelstam 2004).

Meurant et al. (2018) tested a suite of methods for selecting subsets of surrogate species from a pool of the regional vertebrate fauna in the Laurentian mountains of eastern Canada (Quebec).

The authors used data from a comprehensive study that established conservation priority needs based on connectivity analyses of 14 species of vertebrates (Albert et al. 2017), which served as a reference in comparison with other approaches for identifying areas important for landscape connectivity within the 27.000 km² study site. They found that species-based models outperformed habitat-based models, and that a moderate number of species (5-7) could sufficiently capture the GI needs of the broader species pool. Selecting a subset of surrogate species that represented a *diversity of habitat and movement needs* was the best approach, whereas using area-demanding umbrella species or selecting species based on taxonomy performed poorly and lead to priority rank maps that differed considerably from the reference maps (Meurant et al. 2018). While models for some umbrella species agreed reasonably well with the reference maps under certain conditions (i.e. the pileated woodpecker *Dryocopus pileatus* and barred owl *Stirix varia* in scenarios where 10% of the landscape was protected from development), models for the same species showed little agreement with reference maps in other scenarios (i.e., when only 5 % of the landscape is protected). The authors therefore maintain that GI assessments based either solely or predominantly on umbrella species with broad ranges should be avoided.

Krosby et al. (2015) performed a similar analysis, comparing connectivity networks based on species' specific movement needs with networks based on estimates habitat naturalness and integrity. The naturalness-based connectivity networks (i.e. without information on species) are essentially structural connectivity analyses. Their results suggest that at very large spatial scales (greater than all of Norway), habitat-based networks can provide a more *analytically efficient* approach with outputs that agree reasonably well with species' driven reference maps. However, connectivity networks based on all possible combinations of surrogate species all outperformed the naturalness-based models at this scale. At the smaller scale (still nearly three orders of magnitude larger than most Norwegian municipalities), connectivity networks based on all combinations of *4 or more species* outperformed structural connectivity models when compared with referenced networks. These results further underscore that it is feasible to design meaningfully representative connectivity analyses, using only a moderate number of focal species.

Meurant et al. (2018) advocate selecting surrogate species for GI assessment based on the species characteristics that might be vulnerable to the kind of fragmentation occurring within a study site. The habitat preferences of appropriate surrogate species should also correspond with land cover that might be altered by proposed changes in land use, with species' movement abilities corresponding to the spatial resolution of potential management decisions. Because the methods for selecting surrogate species so clearly affects the outcome of connectivity models, Meurant et al. (2018) stress the importance of being explicit about the criteria used. Their recommendations are consistent with points we make in describing the first step of the protocol we present for assessing GI (Chapter 3.1). Assessments need to begin with a deliberation of both the most relevant ways GI can be expected to affect an area's biota, in terms of *specific ecological processes*, and of how potential changes in either land use or climate might impact GI quality and connectedness.

It would not be ecologically meaningful to suggest a set of species that all Norwegian municipalities should use for their own GI assessments. Norway spans an enormous environmental gradient, and different municipalities often contain vastly different species assemblages. However, if GI assessments are to be implemented for each municipality in Norway, the first phase of this national-scale effort should be to identify species with habitat preferences and movement capacities that would render them suitable as focal species for GI assessments of Norway's municipalities. Information on suitable focal species can be stored in a database with links to the ecological data necessary for generating habitat preference and landscape friction models. It would be ideal if potential focal species have positioning (GPS or radio tracking) data, since these data allow us to generate input layers for GI assessment with less (and quantifiable) uncertainty. Ultimately, the decision of which species or array of species should be included in a municipality's GI assessment should result from a dialogue involving planners, land managers, biologists familiar with candidate species, GI-modellers and stakeholders.

2 Conceptual components and state-of-the-art of green infrastructure assessment

Green infrastructures are essential for both biodiversity conservation and human well-being. GI are also very broad and multifaceted concepts that do not fit neatly into the domain of a single science or research discipline. GI are effectively a synthesis of the complexity of ecological and human functional interactions in real landscapes, and it is particularly challenging to capture it under one theoretical and methodological framework. Furthermore, the concept of GI is still relatively new, and the scientific community is only now starting to organize itself to tackle this highly interdisciplinary challenge. Consequently, there are no widely accepted scientific methodologies for quantifying GI (European Commission 2012). Still, the importance and urgency of finding sustainable solutions for GI management has led to a surge of GI initiatives worldwide based upon the best available knowledge, practices, and available scientific tools from a range of disciplines.

We propose a general work flow for spatial modelling of Green Infrastructures to estimate habitat connectivity for biodiversity (**Figure 2**). This approach can also be applied to assessing the biophysical attributes that provide ecosystem services. We refer to this modelling process as GI assessment, because it both identifies where GI is located and quantifies the contributions landscape elements make for providing well-connected suitable habitat. The modelling framework we present builds on GI assessment guidelines from the European Environmental Agency (EEA 2014), while integrating recent advances from several disciplines. In the past decade, science has made tremendous progress in formally integrating existing research fields, developing robust and comprehensive approaches to aid the spatial analysis of GI. Green infrastructures integrate and scale-up two main ecological components: **habitat quality** and **movement-based connectivity**. These conceptual building blocks stem from several different research fields—niche modelling, landscape ecology, network theory and movement modelling—all of which have seen rapid developments in the past decade. Here we present a general overview of relevant concepts and approaches for each of the conceptual components—the building blocks—required for GI assessment: habitat quality and connectivity. We briefly describe the state-of-the-art regarding the recent integration of these building blocks, relying on recent advances in computer science and network studies that enable computational feasibility over large, real-world landscapes at high resolution. This is a rapidly-advancing area of research, and we can expect progress in the coming months that can help Norwegian municipalities, counties and state agencies achieve their GI modelling goals for land planning for even larger areas, at higher spatial resolution and with faster computation time.

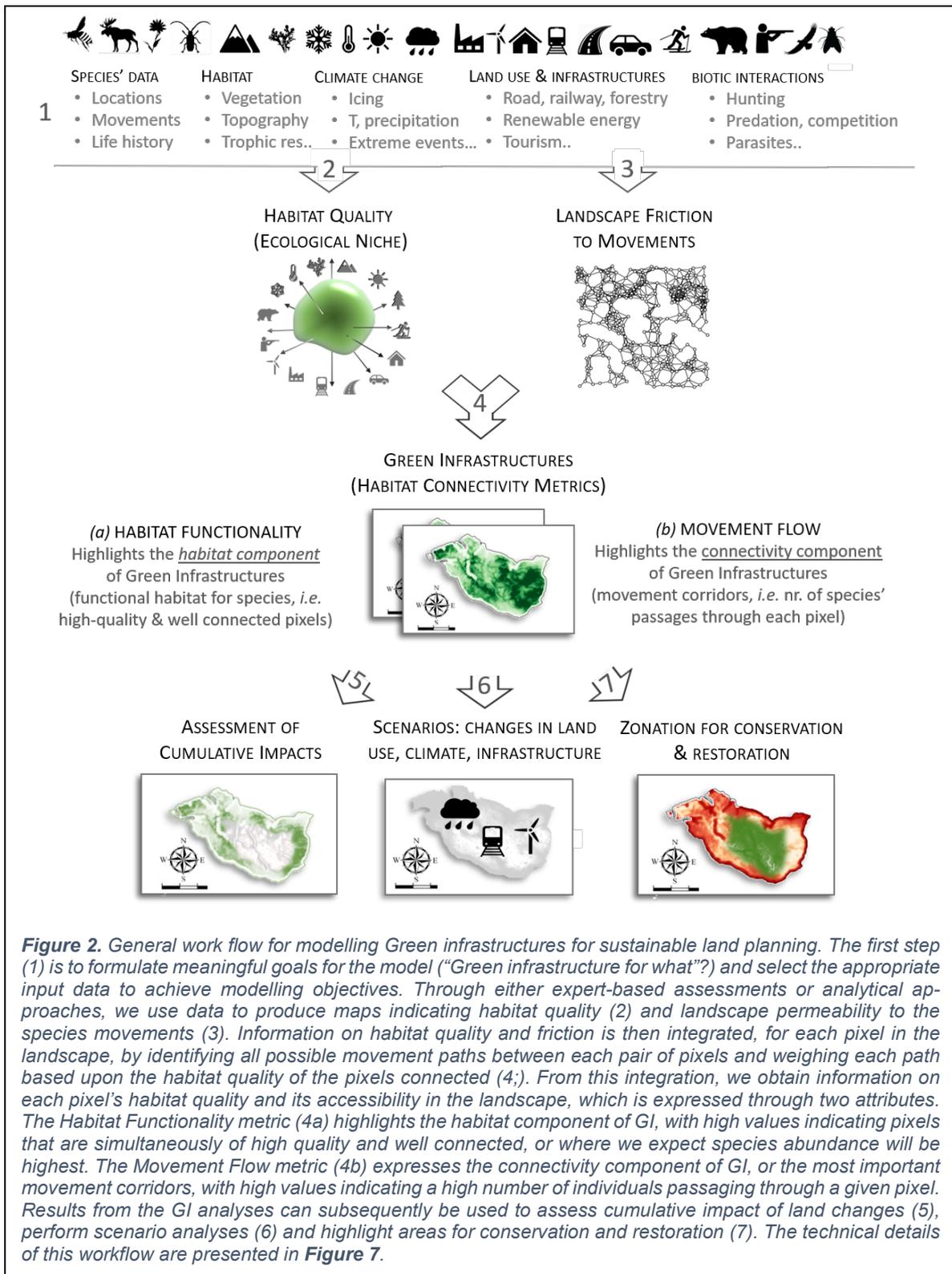


Figure 2. General work flow for modelling Green infrastructures for sustainable land planning. The first step (1) is to formulate meaningful goals for the model (“Green infrastructure for what?”) and select the appropriate input data to achieve modelling objectives. Through either expert-based assessments or analytical approaches, we use data to produce maps indicating habitat quality (2) and landscape permeability to the species movements (3). Information on habitat quality and friction is then integrated, for each pixel in the landscape, by identifying all possible movement paths between each pair of pixels and weighing each path based upon the habitat quality of the pixels connected (4;). From this integration, we obtain information on each pixel’s habitat quality and its accessibility in the landscape, which is expressed through two attributes. The Habitat Functionality metric (4a) highlights the habitat component of GI, with high values indicating pixels that are simultaneously of high quality and well connected, or where we expect species abundance will be highest. The Movement Flow metric (4b) expresses the connectivity component of GI, or the most important movement corridors, with high values indicating a high number of individuals passaging through a given pixel. Results from the GI analyses can subsequently be used to assess cumulative impact of land changes (5), perform scenario analyses (6) and highlight areas for conservation and restoration (7). The technical details of this workflow are presented in Figure 7.

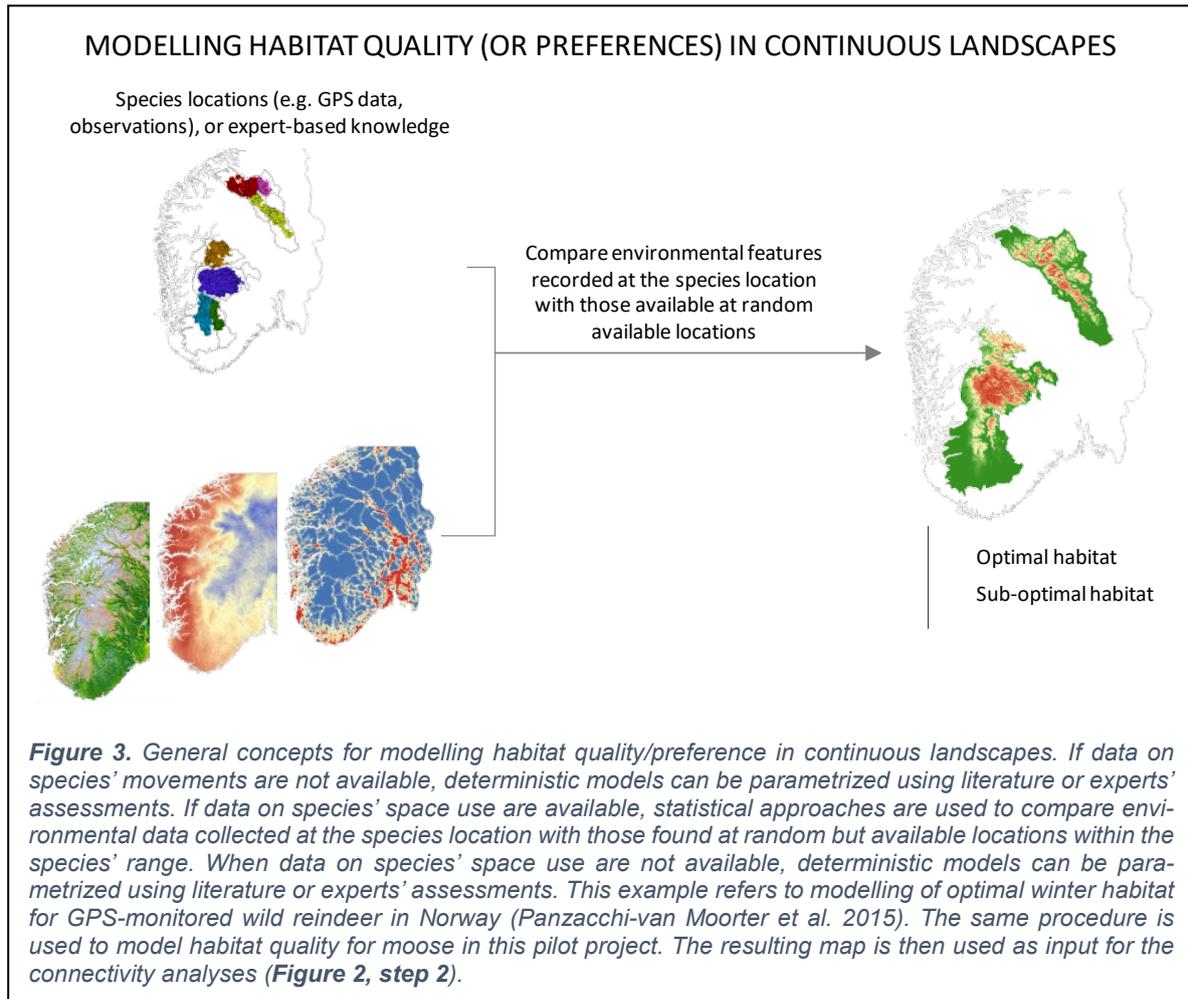
2.1 Habitat quality

Habitat quality refers to a combination of landscape features that provide the crucial resources required for long-term persistence of a species or ecosystem. Because the information we frequently use to describe habitat quality (spatially explicit species abundance data) are not an objective measure of quality, many authors use the term *habitat preference* instead. “Core areas” is a common term for describing areas with high habitat quality. In the simplest approaches, such areas are defined by designated protected areas or other important habitat patches as identified by experts. Connectivity analyses would then treat these core areas as discrete patches of habitat immersed in an unsuitable matrix through corridors.

However, real landscapes are more complex than discrete representations of “habitat” or “no habitat”. Habitat quality (or preference) generally varies along a gradient from completely unsuitable to optimal (or most preferred) habitat, and this variation along a continuum matters to organisms’ use of the landscape. *Ideal Free Distribution* is the ecological theory describing how organisms tend to distribute themselves spatially based on resource availability (Fretwell & Lucas 1969). Organisms’ population density generally varies proportionally relative to the habitat suitability. Density is generally highest in optimal habitat, but organisms often persist in lower densities in habitat with comparatively lower suitability. This theory implies that areas featuring sub-optimal habitat may be important for species’ local population dynamics because they can still provide adequate resources for a lower density of individuals. Patches of highest quality habitat can be “sources”, where positive local population growth rates produce a surplus of individuals that disperse to other patches and contribute to gene flow. Individuals may, however, still use and persist in areas that feature conditions that might be comparatively less favourable for organisms’ survival, growth and reproduction.

Therefore, GI assessment is more realistic when based on a **nuanced, continuous representation of the species’ habitat quality and not simply a binary delineation of core and non-core areas**. Such continuous estimates can be produced by using data on species locations. When data on species’ space use are not available, deterministic habitat quality models can be parametrized with information gathered from the scientific literature or by using experts’ assessments of species preferences for different land cover categories and then classifying land cover data accordingly.

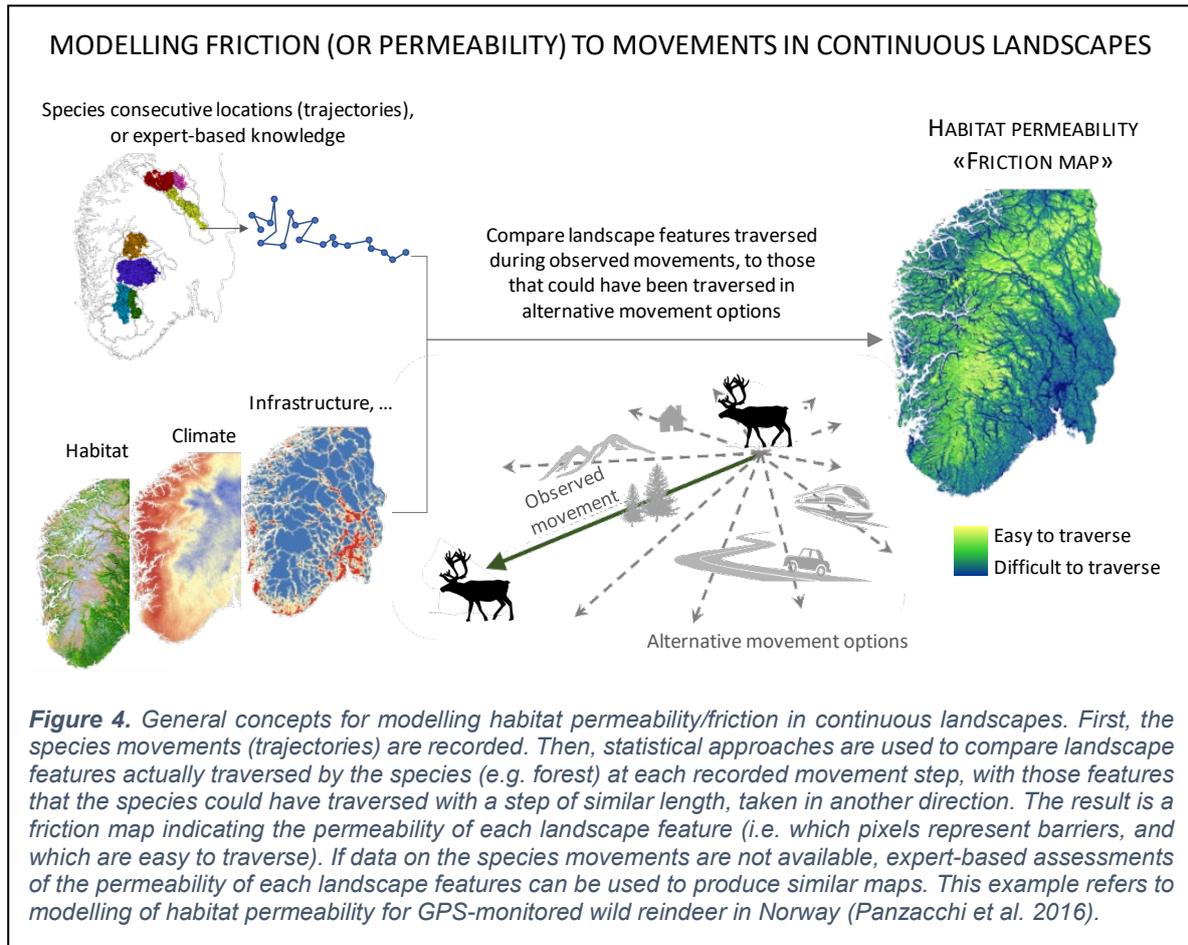
If data on species’ locations (e.g. GPS data, observations) are available, habitat preference maps are typically produced **through stochastic modelling of the “ecological niche” of species or ecosystems**. Most ecological niche models use a correlational approach and quantify habitat quality by determining the environmental conditions (climate, land cover, infrastructures and other relevant biotic or abiotic data) that influence species’ space use. Such approaches combine animal locations with environmental data at these locations to understand which habitat types the species prefers (**Figure 3**). Commonly used analytical methods include Resource Selection Models (Panzacchi et al. 2015), Resource Selection Probability Functions (Sólymos & Lele 2016), Species’ Distribution Models (Thuiller et al. 2009), and Environmental Niche Factor Analyses (Hirzel et al. 2002). The models identify the conditions a given species or ecosystem needs for existence, describing habitat quality as a function of variation in the environmental conditions (**Figure 3**).



2.2 Connectivity

Landscape connectivity addresses the potential that species can move freely between areas that provide important resources. Connectivity is determined by permeability (the inverse of friction) and movement corridors (the inverse of barriers). Although these concepts are closely related, they refer to different spatial scales and distinct ecological processes. *Permeability refers to the capability of an individual to take a step traversing either a natural or man-made landscape feature* (e.g. can a moose walk through a big rock, or through deep snow?). Hence, friction simply describes the degree to which each landscape feature (e.g., roads, slopes) has the *potential* to hamper *hypothetical* movements. Permeability does not, however, address the probability that individuals *in fact* move through that part of the landscape. *Movement corridors refer to the likelihood that the species would actually move through a given area in the landscape to reach important resources* (e.g. where are the most likely movement or migration corridors for moose?). Understanding these differences is crucial in order to correctly assess connectivity (**Figure 4**).

Connectivity analysis therefore consists of a **two-step process**. First, it is necessary to estimate to which degree each landscape feature represents obstacles or resistance to fine-scale movements (steps). The resulting map of landscape **friction** is one of the two inputs required in GI assessment. Only then can we apply algorithms describing a focal species' movement patterns, and mathematical formulas linking movement patterns to the distribution of resources ("habitat quality") in the landscape, to identify areas with the highest probability of movement flow—or movement corridors.



2.2.1 Friction and permeability

The first step to assess connectivity is to estimate landscape friction. Friction and permeability are estimates of **the degree to which each landscape feature might either hamper or facilitate organisms' movements across it**. Species do not move evenly across the landscape. First and foremost, individuals are simply not capable of moving equally well through natural or man-made features in the landscape. For instance, it may be impossible for a moose to walk through a fence, a building, or a cliff (very high friction). Similarly, a moose might be able to climb a steep slope or walk through areas with deep snow (medium friction) but, given the choice, it would rather move through an easier terrain (low friction). Movement decisions are therefore influenced first and foremost by the degree of permeability of the landscape features of an individual's immediate surroundings, depending on the species' capability to traverse a given feature and by the other movement options available to an individual at a given place.

Continuous friction maps describing the permeability of each pixel in the landscape can be produced either using data on individual trajectories or literature and expert-based assessments if trajectory data are not available.

The availability of high-resolution, individual tracking data in ecology is relatively recent, as such data became available only in the past decades thanks to advances in remote sensing-based tracking techniques. GPS tracking methods were initially only applicable for larger species. However, we now see individual movement data available worldwide for a variety of mammals, birds and fish—with promising results in insect tracking as well. Tracking data enable the study of individuals' trajectories with respect to both the landscape characteristics individuals traverse

and those they avoid, allowing us to obtain a mechanistic understanding of the permeability of different elements of the landscapes (e.g., Beyer et al. 2016). We can now estimate how permeable different infrastructures or landscape features (e.g., roads, rivers) are to individuals' movements for a wide range of species. The analysis of data on species' trajectories (e.g., GPS tracking data) is the most robust approach to generating landscape friction maps. Step Selection Functions (Panzacchi et al. 2016) are a special type of the popular Resource Selection Functions that can be used to compare landscape features traversed during an observed step with the landscape features that could have been traversed if the individual would have chosen to perform an alternative step (**Figure 4**). This allows to calculate the probability of traversing each landscape feature, and these probabilities can be used to produce maps illustrating the permeability at each pixel.

If data on species' space use are not available, friction maps can still be produced by classifying available environmental data (land cover, infrastructures, climatic data and other relevant biotic or abiotic data) based upon parameters from the scientific literature or from expert assessments on the species' movement abilities. This is the equivalent to estimating habitat quality using similar sources, except that landscape friction parameters reflect the ability of the individuals to traverse each landscape feature.

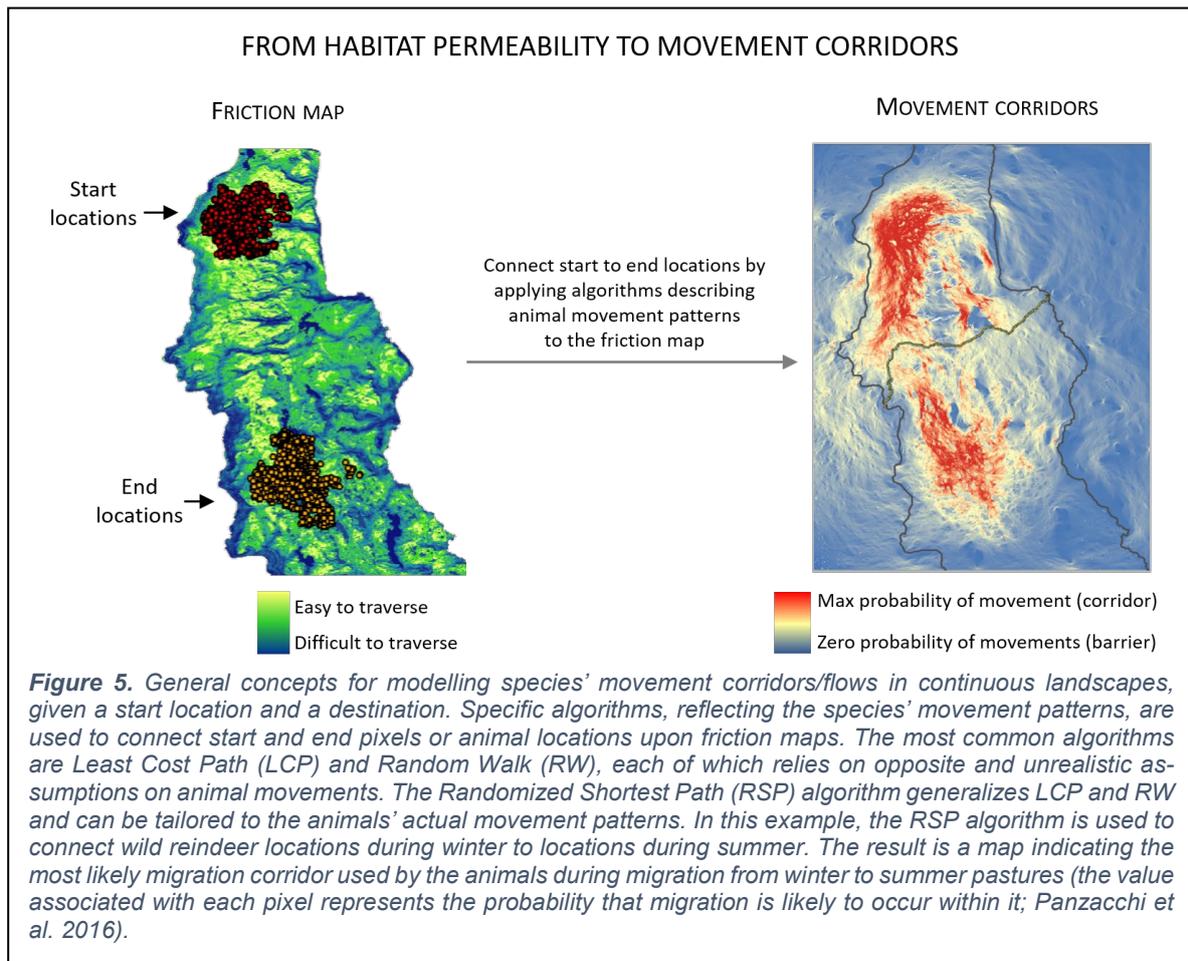
2.2.2 Corridors and barriers

With a friction map in place, the next step is to assess whether each of the hypothetical steps an individual *could* take are likely to occur. Even if an individual is capable of traversing a given landscape feature, it is not a given that it will do so if the area on the other side of a landscape feature is not appealing. For example, a river may pose relatively low friction to a species' movements, but they may act as barrier if the animals have no reason to reach the other side. Individuals generally move for specific reasons (e.g., to forage or disperse) and tend to choose specific movement corridors over other possible alternatives. **Movement corridors are areas where movement is not only possible (i.e. friction is not too high), but it is also most likely.** To identify movement corridors, it is necessary to understand not only the movement capabilities, but also the **motivations** underlying species movements (i.e. the distribution of resources, or high-quality habitat), and the **species' movement patterns** (e.g. directionality of the movements, energetic cost of movements).

Earlier studies tended to describe corridors as "last resorts to counteract isolation of populations inhabiting habitat patches" (Hobbs 1992), or "bandages for wounded landscapes" (Laurance and Laurance 2003). Numerous attempts have been made to characterize corridors using specific physical attributes. Corridors have been defined as linear (Rosenberg Noon & Meslow 1997) or non-linear features (Anderson & Jenkins 2006), spatially explicit (Hector et al. 2007) or diffuse (Hargrove et al. 2005), lines (Hobbs 1992), narrow strips (Soule & Gilpin 1991) or wide regions (e.g. cross-hemisphere corridors; Bairlein et al. 2012), continuous (Tischendorf & Fahrig 2000) or discontinuous (i.e. based on stepping stones; Bennet 2003), long (Gill et al. 2009) or short (e.g. wildlife overpasses; Williams & Snyder 2005), natural or artificial, and characterized as containing both good and low quality habitat (Haddad & Tewksbury 2005; Kuefler et al. 2010). Some authors define corridors as temporary conduits for animal movements (Hess & Fisher 2001), while others describe them as broad areas containing a species population's entire home range (Fraser et al. 1999; Haddad & Tewksbury 2005).

Recent advances in animal tracking technologies have brought a transformation in how we conceptualize animal movement corridors. Authors now seek a more inclusive definition for corridors, shifting the focus from the physical features of the landscape onto the attributes related to the interaction between species and their environment. Popular definitions of corridors now include any regions that facilitate the flow or movement of individuals, genes, and ecological processes (Chetkiewicz, St. Clair & Boyce 2006; Hilty et al. 2006; McRae et al. 2012). If corridors can be the areas where a flow of genes or individuals occurs between areas, then barriers are

the areas that impede such flows (Panzacchi et al. 2015). Corridors and barriers essentially constitute two ends of a continuum: a “single, inextricable element shaping the distribution of individuals and species at multiple scales” (**Figure 5**; Panzacchi et al. 2015). Corridors can thus be any shape and size, high- or low-quality habitat, diffused or demarcated, continuous or discontinuous, static or dynamic in space and time—provided they allow movements between functional areas. It also follows that individual or species’ ranges can be regarded as an assemblage of spatiotemporally dynamic functional areas that are connected (or separated) by spatiotemporally dynamic corridors (or barriers). Indeed, some authors define corridors as temporary conduits for animal movements (Hess & Fischer 2001), while others describe them as broad areas containing a species population’s entire home range (Haddad & Tewksbury 2005).



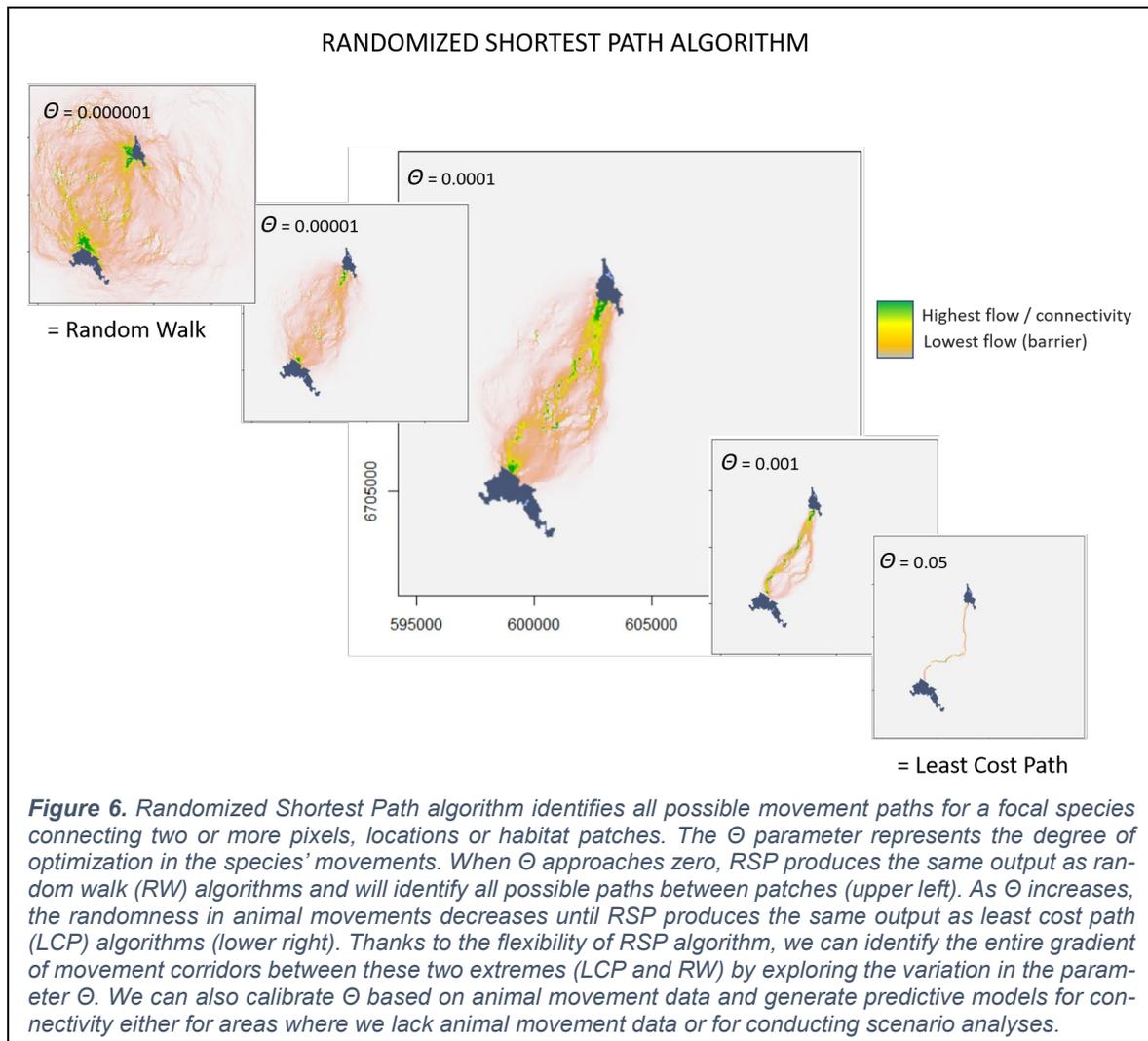
There are many different algorithms used to model potential movement corridors, all of which run upon underlying friction maps. One of the simplest is the **Least Cost Path (LCP)**. LCP simply assumes that species will opt to move through the single, shortest and narrow (1-pixel width) path that connects two areas (Carroll et al. 2012, Pinto & Keitt 2009). Inherent in this assumption is that habitat quality is an important determinant of corridors, that corridors are narrow, and that individuals have complete knowledge of the entire landscape and are thus able to select the shortest, 1-pixel path with the highest quality habitat. A consequence of this unrealistic assumption is that LCP ignores all alternative routes, stepping stones and the wider corridors. In some contexts, this can result in either an overestimation or—more frequently—a substantial underestimation of the actual connectivity between areas. Additionally, LCP is highly sensitive to classification errors in the friction maps.

The European Environment Agency recommends that conservation advice should not be based on single pixel lines derived by LCP (EEA 2014). As a potential work-around, analyses involve widening the one-pixel LCPs, and assessing the surrounding habitats to see if they also could represent corridor swaths that could be appropriate for migration (EEA 2014). Yet this simple solution may overlook other potentially important corridors that are not adjacent to the LCP. Nonetheless, many studies continue to use LCP-based algorithms for their simplicity and computational feasibility.

Random Walk (RW) based algorithms represent an alternative capable of overcoming some of the limitations of LCP. In connectivity studies, a RW is a stochastic, mathematical process describing a path consisting of a succession of random steps taken on friction maps. A RW-based algorithm assumes that individuals only have knowledge of their immediate surroundings, and therefore move “at random” (McRae et al. 2008, Ovaskainen et al. 2008, Tang & Bennett 2010). RW algorithms are sometimes called the “drunkard’s walk” (Weiss 1983). RW models also make their own unrealistic assumptions about animal movements. Most species do not move at random, but rather exhibit some directionality to avoid taking the longest route to get from one place to another. An individual executing a random walk may also tend to “get lost” in large landscapes. Using this algorithm in connectivity studies can highlight one or several “corridors to nowhere”.

The two algorithms essentially make opposite assumptions about individuals’ movements: LCP assumes optimal movements and RW assumes random movements. Consequently, LCP- and RW-based analyses can lead to conflicting prioritization of areas for landscape connectivity. Several studies have tried an ad-hoc combination of the two different approaches in an effort to bridge the divide between LCP and RW, such as applying each to a different scale (e.g., de la Fuente et al. 2018). However, the absence of a formal integration process increases the probability of producing errors and inconsistencies and the resulting process is poorly suited for either automation, repeating the analyses with updated data or applying the approach to different analytical contexts.

Perfectly optimized movements (LCP) and perfectly random movements (RW) represent the two ends of a continuum describing how animals might move in space. While some species exhibit movement that reasonably resembles either one or the other extreme, **most species likely move in a way that is somewhere in between optimal and random steps**. Our research team recently proposed the use of the **Randomized Shortest Path (RSP)** algorithm to bridge the gap between the opposite assumptions of LCP and RW model movement paths (Panzacchi et al. 2016; **Figure 6**). RSP formally integrates LCP and RW approaches, by modelling the degree of randomness in animal movements through a single parameter, Θ (Kivimäki et al. 2014, Panzacchi et al. 2016, Saerens et al. 2009). One can calibrate Θ so that connectivity models agree with animals’ observed movement patterns, thereby generating a predictive model that is far better equipped to highlight the most realistic movement corridors than either pure RW or LCP approaches can (**Figure 6**). The RSP algorithm has been developed in collaboration with computer scientists, and it is optimized for efficient computation in high-resolution large landscapes. This is crucial for applying the analyses to actual landscape planning cases.



2.3 Integrating habitat quality and connectivity in GI modelling

Habitat quality maps are necessary for identifying species' core areas, but alone they are not sufficient to correctly identify priority areas for conservation. If a patch of high-quality habitat is inaccessible, movements of organisms to and from the patch may be inadequate to provide species' long-term persistence. Maps identifying corridors and barriers are also necessary for identifying where organism movement can take place, but we cannot understand landscape connectivity if we do not also consider the quality of the habitat patches that they connect. For example, mitigation measures like road overpasses may be ineffective conservation measures if they connect low-quality habitat. GI assessment requires formally integrating information on both habitat quality and movement-based ecological connectivity.

Until 2007, there was no way to formally integrate habitat quality and connectivity within GI assessment. While Hanski and Ovaskainen (2000) developed Metapopulation Capacity (MC) to assess the consequences of fragmented landscapes on species' population dynamics, the approach is impractical for large landscapes due to its computational complexity. This shortcoming stems from the different theoretical backgrounds and methodologies for estimating habitat quality and connectivity. Habitat quality studies typically use niche modelling approaches to quantify the relationship between species' occurrence and environmental characteristics (Kearney 2006). Connectivity studies generally use graph theory (Cantwell & Forman 1993, Urban & Keitt 2001), assessing networks with graphs consisting of a set of *nodes* that represent habitat patches and

the *links* that form the connections between them. Yet linking the niche-based models of habitat quality with network theory movement models is not straightforward.

Saura and Pascual-Hortal (2007) provided a major breakthrough by developing the mathematical formula to combine habitat quality and dispersal probability within a graph theory framework. Their Probability of Connectivity (PC) metric simultaneously expresses both the *amount of good-quality habitat and its connectedness*. In the decade since it first was introduced, the software which implements this PC metric (CONEFOR) has been used in more than 200 studies worldwide (Saura et al. 2018)—including the study that the Norwegian Environmental Agency indicated would be an appropriate model for this project (de la Fuente et al. 2018). CONEFOR is also being considered (European Commission 2012) for the assessment of the 2011–2020 Strategic Plan for Biodiversity’s Aichi Target 11 (CBD 2010), which aims at the expansion of well-connected protected areas at a global scale (Saura et al. 2018).

Despite its popularity in landscape ecology, the CONEFOR software represents animal movements simplistically, using the LCP algorithm described above. A growing number of studies on animal movement corridors therefore rely on another software application, CIRCUITSCAPE, that represents animal movements using a RW-based algorithm (McRae & Beier 2007, McRae et al. 2008). CIRCUITSCAPE has become extremely popular in movement ecology and has been cited in over 800 studies (Marrotte & Bowman 2017) in the decade since it was introduced. However, CIRCUITSCAPE lacks a formal integration of habitat quality and connectivity.

Authors of this report currently collaborate with the developers of both CONEFOR and CIRCUITSCAPE, with the goal of integrating their respective approaches and software using the RSP algorithm (**Figure 6**). By integrating the RSP algorithm (Panzacchi et al. 2016) with the PC metric (Saura & Pascual-Hortal 2007) and extending the computations to all pixels in a landscape through centrality metrics, we can produce a more realistic representation of species’ movements in connectivity studies and more robust representations of GI (Van Moorter et al. 2016, Van Moorter et al. 2017b, Van Moorter et al. 2017a).

3 Protocol for modelling Green Infrastructure

We propose a protocol for modelling Green Infrastructures that builds from the general EEA guidelines (2014) and incorporates several recent technological and theoretical advancements. In this chapter, we describe the steps for the modelling sequence adopted in this report and illustrated in **Figure 2** to model GI. The protocol models GI for a specific species or ecosystem in specific landscapes. We also indicate how model outputs could be further utilized to generate decision-support maps in planning for landscape connectivity at a municipal level or at larger scales. We provide additional detail for each step within the context of example models in Chapter 5.

3.1 Step 1: Formulate specific goals and identify appropriate data

The process for assessing GI begins with identifying and articulating the motivation or goals for the project. Goals should be clearly stated and measurable, so that one can assess the success of implementation (Beazley et al. 2010). The results we produce are designed to support sustainable land-planning, and it is therefore necessary to be explicit about which decisions need this information. The scale of the focal land planning area, the heterogeneity of the landscape, the temporal perspective and the ecological goals will, to a large degree, determine the level of resolution (spatial, temporal and taxonomical) necessary for producing an appropriate model of the GI that can best meet the specific information needs.

Part of this initial step is defining which focal species, species assembly or ecosystem to model (see also Chapter 1.5). Note that if the aim is to prioritize GI for biodiversity in general, the best option would obviously be to protect all areas. As this is generally unfeasible, we need to prioritize conservation objectives, and identify potential constraints. For land planners who seek to simultaneously identify GI for several species with different habitat preferences, the models might suggest that almost the entire landscape needs protection. The focal species should be relevant for the conservation or land-planning objectives: what types of habitats will be affected by changes in land management, and which species might be vulnerable to the resulting fragmentation? Part of identifying a focal species for the model involves considering which of the ecological processes are influenced by connectivity and how alternative land management options might potentially influence the species' persistence in the landscape. For example, do we want to facilitate organisms' dispersal and colonization of remote areas, movement within the home range of a resident species, preserve migration between seasonal habitats, or avoid genetic isolation and ensure maintenance of metapopulation dynamics? The ecological process of interest for the model will affect decisions regarding the spatial extent of the study area and the movement related model parameters.

Focal species should also be selected such that the set of species for a municipality's models can account for all areas in a municipality that have presumed importance for GI. This will enable the GI modelling to incorporate these geographic structural elements of GI in the context of the species who live or move within with these areas and the relevant ecological processes. Purportedly important structural elements thus serve as the input layers that describe habitat quality and landscape friction for GI models for one or several focal species for a municipality's set of surrogate species. A set of surrogate species for any given municipality would not be complete if the structural elements initially identified as purportedly important components of GI aren't used as a model input in for at least one focal species model.

The intended purpose or goals of a GI model must match the data available for inputs, which is why we present goal formulation and data selection as two components of the same step. For each focal species' GI model, we need to identify which datasets suitably capture the relevant attributes in the landscape and influence both organisms' habitat quality and movements at multiple scales. Landscape connectivity has many facets, even when it is considered within the

context of a single focal species. The spatial resolution and extent of data must also correspond to the focal species' habitat requirements and capacity for movement, as well as the potential strategies for GI management.

3.2 Step 2: Estimate habitat quality

It may be tempting to attempt to identify high-quality habitat using *administrative boundaries* referring to designated areas that are under varying level of protection (e.g., Ramsar, Natura 2000, Emerald Network, national parks) or are otherwise formally recognized as important for biodiversity. Framstad et al. (2018) provide guidelines for potential criteria that could be used to identify core areas based on their importance to biodiversity. The authors also identify examples of administrative boundaries that may be relevant in a Norwegian context. For the most part, these criteria reflect a qualitative approach that treats areas as either suitable or not suitable for species or overall biodiversity, thereby relying upon assumptions whose validity may be difficult to assess. As explained in Chapter 2.1, this will substantially reduce the power and scope of connectivity analyses, and possibly lead to incorrect prioritization of conservation areas and ineffective strategies. For this reason, we recommend using data-driven approaches wherever possible.

More nuanced, continuous estimates of habitat quality can be produced using information on the species' preferences for each available landscape feature. In the absence of data on species' locations, these estimates can be obtained based upon expert-opinion and the scientific literature, as we did in our example on winged forest insects associated with older conifer forests. The output of this procedure is similar to a data-driven habitat preference map. However, one must remember that because the association between habitat and species has not been estimated using data and statistical procedures, it is not always possible to assess the accuracy of such results.

Alternatively, we can produce more robust habitat preference estimates through statistical analyses if data on the species' locations are available. In the model we present for moose, we used GPS data with Resource Selection Probability Functions (Sólymos & Lele 2016). This is an improved version of simple Resource Selection Functions (Aebischer et al. 1993, Panzacchi et al. 2015), that allows estimating absolute (rather than relative) probabilities of habitat selection. Alternative approaches that could be used for this purpose include species' distribution models (Thuiller et al. 2009), and Environmental Niche Factor Analyses (Hirzel et al. 2002). Ideally, results on habitat preferences should be supported by data describing how species' reproductive fitness (i.e., per capita population growth rates) vary as a function of the environmental conditions.

3.3 Step 3: Estimate landscape friction

Continuous maps representing landscape friction to movements can be produced both through expert assessment or, if data on the species' trajectories are available, through statistical modelling.

In the absence of high-resolution data on species' movements (e.g., hourly GPS locations), friction maps can be obtained based upon expert-opinion and the scientific literature. In our example on forest insects we used published and expert-based information on the ability of such insects to traverse each landscape feature, and we classified relevant environmental layers accordingly.

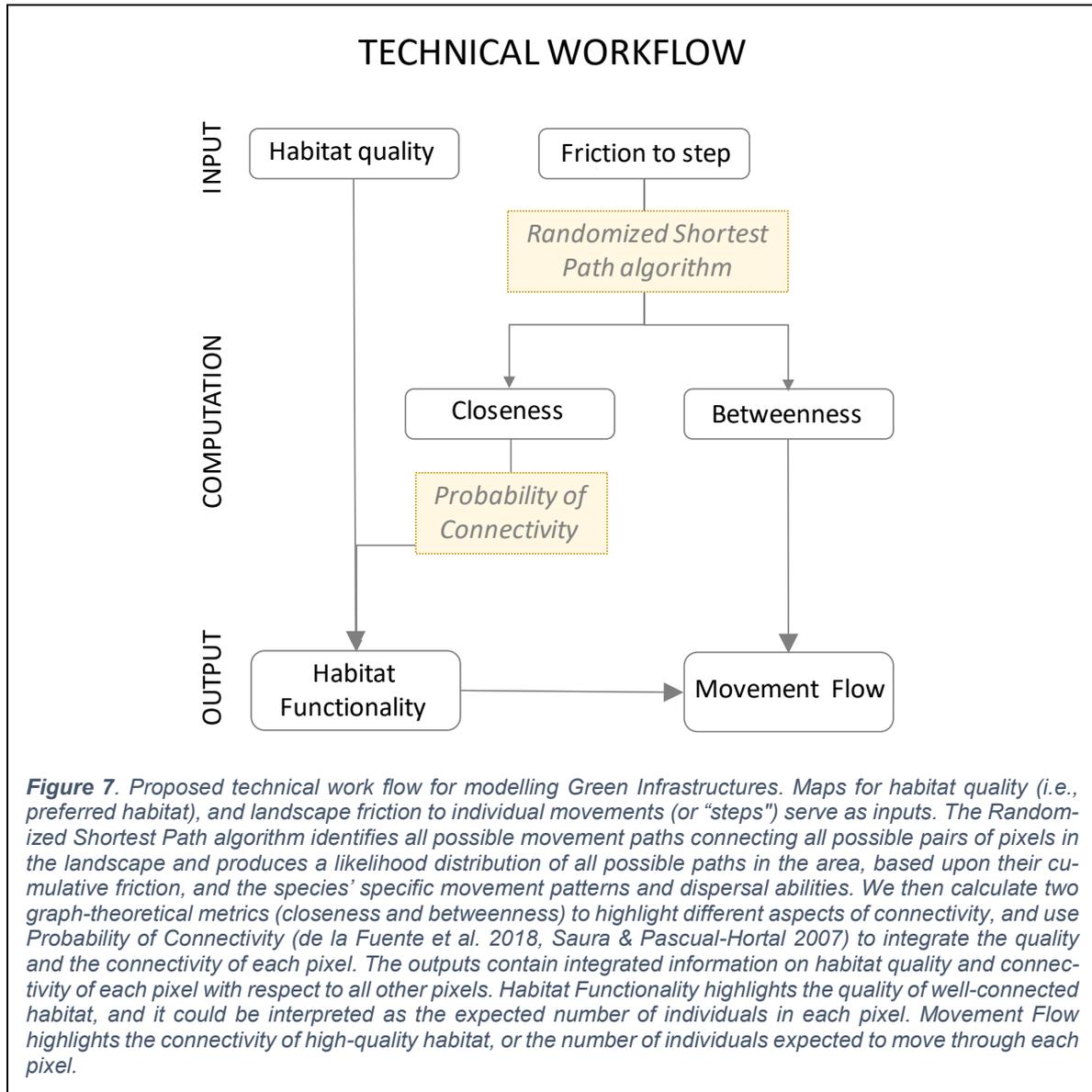
If high-resolution movement data are available, we recommend to use statistical models, and in particular Step Selection Functions (SSF; reviewed by Thurfjell et al. 2014). SSF compare the landscape features traversed by an individual between consecutive locations with the landscape features that the animal would have encountered if it had performed a step of similar length from

the same origin, but in a different direction (**Figure 5**). Using such an approach, it is also possible to estimate the effect of increasing use intensity in such infrastructures (e.g., increase in car traffic along roadways, or an increase in the number visits to cabins or ski trails), or the effect of alternative types of landscape features (e.g., different types of roads, different types of wildlife overpasses, different types of rivers). We can use these estimates to predict friction in each pixel, thus generating “friction maps” representing landscape permeability to the movements of the focal species, as described in Panzacchi et al (2016). The values for each pixel in a friction maps reflect how easy it is for an individual to traverse each given pixel (**Figure 5**).

3.4 Step 4: Model Green Infrastructures

Once habitat quality and landscape friction to movements have been estimated for each pixel in the landscape, these measures need to be integrated and upscaled to obtain a realistic representation of high-functional areas and connecting corridors between them: the definition of GI. We propose an approach that generalizes the Probability of Connectivity (PC) metric (Saura & Pascual-Hortal 2007) by explicitly integrating more realistic estimations on the movement patterns and dispersal abilities of the focal species (see Chapter 2.3). We provide a technical overview of the workflow, omitting mathematical formulas from the main text of the report. More technical details and mathematical formulas can be found in van Moorter et al. (in prep.), and we will share the Python code upon request. Our approach builds on two inputs: the quality and the friction of each pixel in a landscape (**Figure 7**). The Randomized Shortest Path algorithm (RSP; Kivimäki et al. 2014, Panzacchi et al. 2016) uses the friction map to identify all possible movement paths connecting all possible pairs of pixels in the entire landscape. We can calibrate the Θ parameter in RSP based on species observed movement patterns, to highlight the most realistic paths (Kivimäki et al. 2014, Panzacchi et al. 2016, Saerens et al. 2009). The procedure produces a likelihood distribution of all possible paths in the landscape, *i.e.* the likelihood of each path is based upon its cumulative friction and the dispersal abilities of the species. We calculate two graph-theoretical centrality metrics (closeness and betweenness) to highlight different aspects of connectivity. At this stage we integrate the quality of each pixel into these centrality metrics. This is done by applying a mathematical formula (Probability of Connectivity; Saura and Pascual-Hortal (2007) that weighs the closeness and betweenness with the habitat quality of the start and end pixel.

The outputs are two metrics describing each of the two interacting components of Green Infrastructures, quality and connectivity. Both outputs contain integrated information on habitat quality and connectivity of each pixel with respect to all other pixels, and therefore the values attributed to each pixel are based not only on their own habitat quality, but also on the quality of all other pixels in the landscape that are easily accessible from that location.



The potential for species to move in a landscape depends on contributions of two components of GI. The first relates to the contribution that areas make as **source and/or receiver** habitat. The second relates to the contribution areas make as **connectors** between sources and receivers. For areas to function as sources or receivers of moving individuals in a GI, they will need to be both high quality habitat and be well connected to other areas. However, areas with low quality habitat can also contribute to GI by enabling movement between source- and receiver-areas. Effective land use planning will need to consider both components, and our protocol produces two separate but interrelated metrics to assess them. By considering each component with its own metric, planners can acquire a better understanding of the mechanisms through which an area contributes to GI functionality.

Technically, in network theory, the metrics we produced can be described as “*all-pixels centrality metrics*”. This implies that the final value attributed to each pixel, representing the Green Infrastructure, synthesises the properties of all pixels in the entire graph (i.e. landscape), in terms of both habitat quality and movement-based connectivity. As mentioned earlier, this is

computationally challenging, and therefore we established a long-term collaboration with mathematicians and computer scientists to identify *cutting-edge mathematical and computational solutions to allow for computations of movement-based habitat connectivity and Green Infrastructures over large, continuous, high resolution landscapes*.

3.4.1 Output 1: Habitat Functionality

The *Habitat Functionality* metric highlights the habitat quality component of GI, although it contains both information on habitat quality and connectivity. High values indicate **high-quality pixels that are also easily accessible** from all other areas in the landscape. Therefore, higher values indicate highly functional areas where we can expect to find a higher number of individuals. In fact, Habitat Functionality provides a practical estimate of *amount of visits a pixel can receive*, or, the amount of flow that *comes into* a pixel. If a pixel is characterised by poor habitat quality, it would have a low probability of being visited. Similarly, a pixel is not likely to be visited if it is of good quality but very difficult to reach. Hence, Habitat Functionality does not highlight inaccessible high-quality areas (e.g. islands or fenced areas of high-quality habitat).

In network science terminology, Habitat Functionality is an “weighted all-pixels *closeness* centrality metric”, as it measures the closeness (how well connected a pair of pixels are) multiplied by the quality of the start and end node (closeness to poor-quality pixels is less relevant than closeness to high-quality pixels). From a mathematical perspective, Habitat Functionality is a generalization of the Probability of Connectivity (Saura & Pascual-Hortal 2007), that relies on the simple PC for assessing connectivity.

3.4.2 Output 2: Movement Flow

The Movement flow metric highlights the connectivity component of GI, although it contains both information on habitat quality and connectivity. High values indicate **realistic movement corridors, or the expected number of species’ passages (or flow) through each pixel**. In Movement Flow, the quality of the pixel itself is not crucial; a pixel could be of poor habitat quality but still be very important for maintaining connectivity in the entire landscape (e.g. road overpass).

In its simplest form, the RSP algorithm first treats each pixel a potential connector and quality is irrelevant (a pixel can be of poor quality and still be a good connector). This initial result is then weighted by both the quality of the habitat and the closeness of the start and end pixel. This weighting corrects for the tendency of identifying either the rare and extremely long paths or easily traversed paths that link two or more areas with poor-quality habitat. The resulting Movement Flow metric therefore expresses the expected number of passages through a pixel, accounting for both the habitat quality and the closeness of the pixels connected. It represents the **actual corridors or movement flow of organisms**, without overemphasising rare, long trips, or corridors to poor-quality areas.

The Habitat Functionality metric produces maps that identify good quality habitat that is well connected, but it excludes the areas of lower habitat quality that may still be very important for connectivity. The Movement Flow metric produces maps that identify the important connectors that link good quality habitat areas, but the Movement Flow metric does not identify the good quality areas themselves. It is therefore important to use both metrics in a complementary fashion to identify all areas important for species’ movements.

It may be helpful to regard the Habitat Functionality-map as analogous to a map illustrating popular travel destinations, and Movement Flow-map as analogous to airports and highways required to reach those destinations. The Habitat Functionality metric produces maps that identify good quality habitat that is well connected, but it does not focus on areas of lower habitat quality that may still be very important for connectivity. The Movement Flow metric produces maps that

identify the important connectors that link good quality habitat areas, but the Movement Flow metric does not focus on the good quality areas themselves. **Each metric provides information relevant for different aspects of conservation and land planning. It is therefore important to use both metrics in a complementary fashion to identify all areas important for habitat connectivity.**

3.5 Further steps (5-7): use GI in land planning - scenario analyses, cumulative impacts and zonation

The *Habitat Functionality* and *Movement Flow* metrics describe the two interrelated aspects of Green Infrastructures (i.e., habitat quality and connectivity) for a focal species or species group. Aside from its importance as a scientific achievement for quantifying the functional importance of species' habitat, these metrics provide spatially-explicit information that is necessary to **quantify and display potential cumulative impacts on species and ecosystems from planned or expected changes in climate land use or land management.** The proposed GI modelling protocol has been developed specifically as the first step in the sequence of scientific and socio-political assessments required to provide tangible support for land planning through scenario analyses and sensitivity analyses that assess specific areas' importance for conservation and restoration.

A major strength of the entire proposed procedure is its strong theoretical foundations in ecology and network theory that builds on a coherent, formal integration of species-specific models of habitat use and permeability: the two interacting components ultimately determining both species' movement. By understanding the mechanisms influencing GI, we can **predict** how changes in factors affecting these mechanisms (e.g. land use changes) might impact species' distributions and explore scenario analyses that compare alternative land management strategies. This predictive capacity is a major advantage over simpler expert-based models or GIS-based assessments of structural connectivity that lack explicit consideration of the ecological processes underlying loss of functional habitat.

Note that steps 5-7 describe how the GI models of species-habitat functional relationships can be applied to support land planning and are not part of the GI modelling process itself. We have not implemented step 5-7 in the examples provided in this pilot study, nor have we discussed them further in our protocol for modelling GI. Chapter 7 provides detailed description of how results from GI assessments can be used to support land planning (i.e. scenario analyses, cumulative impacts and zonation).

4 Pilot studies: assessing Green Infrastructure for moose, forest insects and bumblebees

4.1 The study area: Ski municipality

The Norwegian Environmental Agency selected Ski municipality as the focal area for this project from a list of municipalities that participated in a separate national pilot project in 2016 to assess municipal plans' suitability as tools for managing biodiversity. The Ski municipality is located to the south east of Norway's capital city and shares a border with Oslo municipality (**Figure 8**). The majority of the municipality's residents live in either the town of Ski (19 000 residents) or Langhus (15 000 residents). Both major roads leading from Oslo through eastern Norway to Sweden—the E6 and E18—pass through Ski, as well as the main Østfold railroad line that runs through eastern side of the Oslofjord. The municipality covers 165 km², with a topography generally characterized by rolling hills and a west-to-east elevational gradient ranging from 128 to 313 meters above sea level. Most of the area is covered by forests (102 km²), with continuous area of productive agricultural lands (38 km²) in the southwestern portion of the municipality (**Figure 9**). Only 14 km² of the municipality's land cover is presently developed.

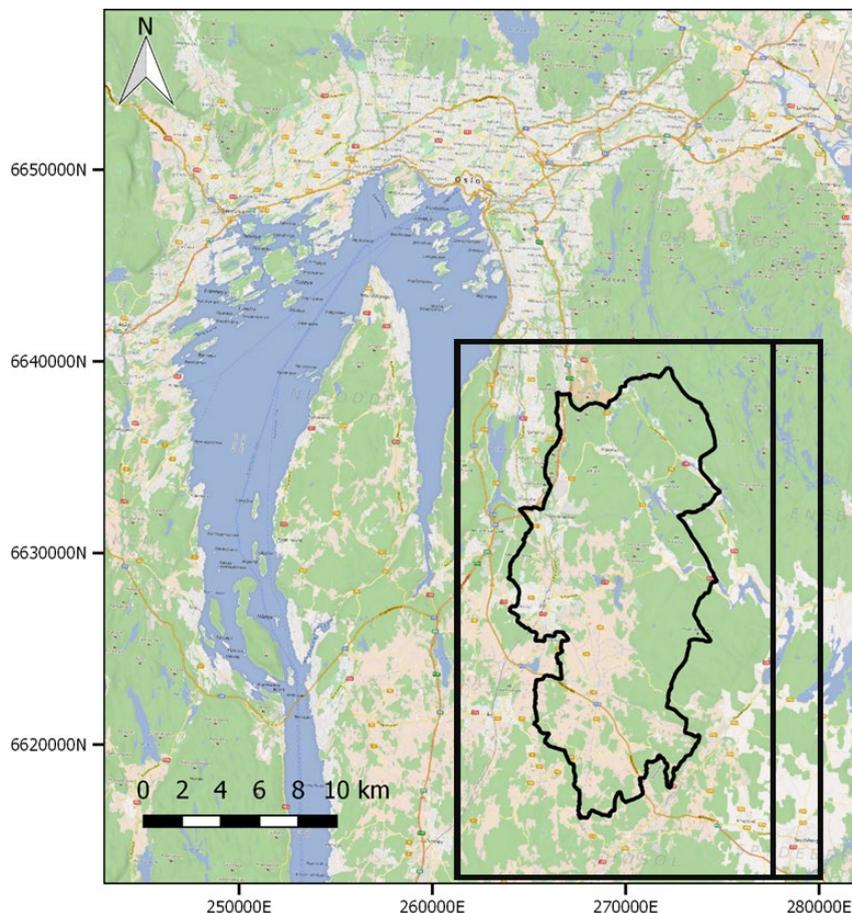


Figure 8. Ski municipality located to the south and east of Oslo, Norway. Black outline depicts the municipality's administrative borders, the extent of the study area used in the analyses for bumblebees and forest insect models (smaller rectangle) and the extend of the area for moose model (larger rectangle).

Ski municipality's proximity to Oslo means that its population could experience an expansion in the coming years. Oslo is projected to grow by between 30 and 40 per cent within 2040.¹ Growth within Oslo will also involve growth in the surrounding counties, such that both Oslo and the neighbouring Akershus county could increase by as many as 260 000 residents by 2030 (Akershus Fylkeskommune & Oslo kommune 2015). Ski is already a one of the largest axes for public transportation within Akershus County. The construction of the Follobanen train line, which will be completed in 2021, will drastically reduce commuting times and make Ski an even more attractive option for housing within a reasonable commuting distance to Oslo. The Follobanen will run parallel to the Østfold line, although much of the line will be underground and should not contribute directly to further habitat degradation and fragmentation.

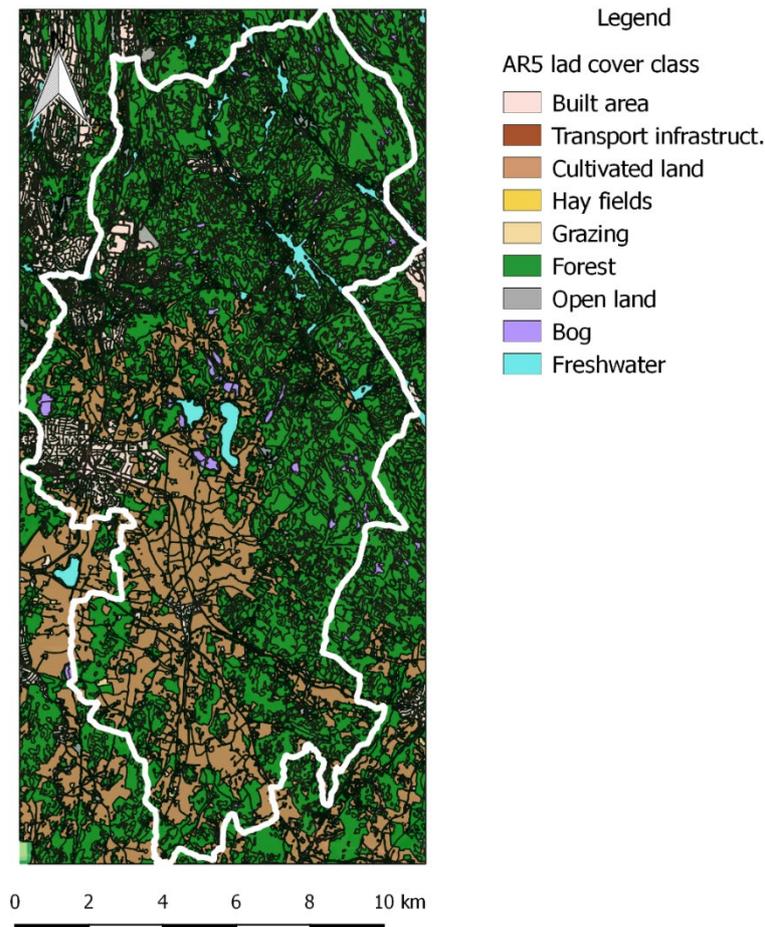


Figure 9. Land cover categories from the FKB AR5 data (as a 1:5000 shapefile) for Ski municipality and portions of neighbouring municipalities. The area shown here corresponds to the extent we used in our connectivity analyses.

The Akershus county governor and the Oslo municipality plan for regional land use and transport (2015) describes a long-term strategy for development in the region that entails delineating both areas where growth is prioritized over protection and areas where conservation of both natural and agricultural areas has higher priority over growth. Ski municipality contains area in both prioritized growth and prioritized conservation groups. Connectivity analyses such as those we

¹ SSB prognosis 1.1.2016. <https://www.ssb.no/folkfram/>

present in this report can help inform how the strategies presented in the regional plan and alternative options within these strategies might impact connectivity of green infrastructure.

Ski and Oppegård municipalities will be united into a single municipality, called Nordre Follo (Northern Follo), from January 1st, 2020. We considered using the new administrative boundaries in our analyses but opted to limit the project to the present Ski municipality for practical reasons related to data processing and the brief duration of this pilot project. Oppegård municipality is located along Ski's western border and covers 37 km². While Oppegård is only about half the size of Ski, the two are comparable in width. Including both municipalities would require that we effectively double the spatial extent of our models: a change that would slow analyses without adding meaningful contributions towards the intended purpose of this pilot project. Note, however, that recent development in modelling methodology should make it possible to adjust our code to perform GI calculations in the broader Nordre Follo area and in other larger regions without drastically increasing processing requirements.

4.2 Environmental data used in example models

Remote sensing techniques are advancing rapidly, with national and international bodies regularly publishing new sources of spatial data that may be appropriate for future GI modelling of Norwegian municipalities. Framstad et al. (2018) provide an extensive list of sources for geospatial data that can be used for assessing Norwegian GI, and we have chosen to not reproduce this list to avoid redundancy. Below we identify and briefly describe the data sources we used in the pilot project's three GI models, providing enough detail for the reader to understand the data's contributions to in the model.

AR5 is the Norwegian National Land Resource Map, with the number 5 denoting a 1:5 000 scale. Land resource maps are also available at coarser scales, but these are not suitable for land use planning. The dataset describes land resources (mainly describing land cover and productivity) based on a standardized national classification system covering all area below tree line. Areas above treeline are listed as "not classified" in AR5. We would need an alternative land resource data source (AR50) for municipalities that have area above treeline. Areas in AR5 are represented as polygons, with a minimum mapping unit of 0.05 hectare (500 m²) for agricultural areas, transport networks and water bodies; 0.2 hectare (2000 m²) for forest, peat bogs and open areas; 0.5 hectare for developed areas and 2.5 hectare for perpetual snow and glaciers. The geometric accuracy for well-defined boundaries is 2 m or better. AR5 is continually updated by municipal administrations and priority is given to agricultural- and urban areas.

SatSkog uses data collected from the Norwegian National Forest Inventory (*Landskogtaksering*) and combines them with land resource maps and satellite imagery to produce a raster layer describing attributes of Norwegian forested land. The database uses a mask derived from AR5 to demarcate forest land cover, so that only the spectral bands from satellite imagery of these areas are included. The dataset provides estimates of dominant tree type (spruce, pine or broadleaf), stand age, standing timber volume, and growth potential for each pixel of forest, based on a set of 1 to 12 neighboring reference pixels. The database is also available as a vector layer, with clustered groups of pixels with like values merged into polygons

N50 was our primary source of spatial data on infrastructure. Attribute themes included in N50 are land cover (water, soil type, etc.), administrative areas, buildings and facilities, height, restricted areas, transport and communications and place names. N50 Map data cover mainland Norway within national borders and the territorial boundaries in the sea. N50 Map data are updated regularly and distributed weekly.

ELVeg provides information on all driveable roads > 50 meters long, the foot and bikepaths, address points, street names, speed limits, traffic control facilities and road restrictions.

Height DTM 10 is the digital terrain model with heights on a 10 x 10 m grid covering all of Norway. Accuracy estimates range between ± 2 to 6 meters, depending on terrain and map data age. The terrain model is suitable for various kinds of terrain visualisation and for calculating terrain slopes and terrain profiles.

Naturbase is a collection of maps administered by the NEA with relevance to natural resource management. Maps with particular relevance to connectivity analyses, and the pilot study areas in particular, include Selected nature types (*Utvalgte naturtyper*), Nature types (*naturtyper*), Cultural landscapes (*Kulturlandskap*), Infrastructure-free natural areas (*Inngrepsfrie naturområder*), Environmental attributes in forests (*Miljøregistreringer i Skog*, also known as *MiS* figures). MiS figures provide information on forest attributes such as rich understory vegetation, coarse woody debris, hollow trees, particularly old trees, etc.: information that is a part of the national forest inventory and thus generally represented in SatSkog data. We did not use most of these maps as actual inputs for habitat quality or friction models, because we were able to verify that the attributes they expressed were already captured in other inputs (AR5 and SatSkog)

Sentinel 2 satellite provided spectral bands used in classifying vegetation cover for a 10 x 10 m grid. We describe how we used this data to capture heterogeneity in vegetation cover within AR5 land cover defined polygons for the bumblebee GI model.

5 Pilot study: Identifying Green Infrastructures for moose, forest insects and bumblebees

Modelling GI first requires identifying the model object. In dialogue with the Norwegian Environmental Agency, we selected three model objects: moose, wood-dwelling insects and bumblebees. These allow us to illustrate Green Infrastructures for two model objects that share—to some degree—similar habitat preferences but have very different movement abilities (i.e. moose and wood-dwelling insects), as well as two model objects that share similar dispersal movement abilities but have largely different habitat requirements. Furthermore, these model objects allow us to illustrate the modelling procedure both when high-resolution individual tracking data are available for the focal species (moose), and when such data are lacking, and models can only rely upon literature and expert-based assessments (bumblebees and wood-dwelling insects). Finally, these examples illustrate the use of single species and of species guilds in the analyses of GI. These three examples illustrate differences in methodological complexity for estimating both habitat quality and landscape friction. **Table 1** provides an overview of the data sources used for each of these three models.

Table 1. Data sources used for either habitat quality (HQ) or landscape friction (LF) components for each of the three models we provide as examples of GI modelling. Chapters 5.1, 5.2 and 5.3 provide additional details about the specific information used from the data sources.

Data source	Moose		Forest insects		Bumblebees	
	HQ	LF	HQ	LF	HQ	LF
AR5	X	X	X	X	X	X
SatSkog	X	X	X	X		
N50	X	X				
ELVeg	X	X				
DTM 10		X				
Naturbase			X	X		
Sentinel2					X	X
Traffic - Statens vegvesen		X				

We chose to not include climatic variables in the example models we describe here for this pilot project, although they might certainly be appropriate for GI modelling efforts in other contexts. If, during the model planning process (**Figure 2, Step 1**), modellers determine that climate is an important aspect of the factors that influence species' distribution and space use within the spatial and temporal context of the analysis, then climate and weather-related data should be included in precisely the same way as other environmental data inputs. Climatic variables can be incorporated both into the habitat quality inputs of GI models, reflecting how climate variables affect the suitability of habitat for a given species, and also into the landscape friction, to reflect how climate affects animal movements directly (e.g., deep snow might hamper moose's mobility in winter, and air temperature can influence flight capacity of winged insects). Explicit incorporation of climate variables can facilitate using model outputs in scenario analyses to explore consequences of climate change on landscape connectivity. However, we can also generate climate change scenarios by expressing the projected effects of a changing climate through other variables (e.g., the corresponding changes in land cover).

5.1 Moose

Moose (*Alces alces*) is an extremely well-studied large mammal, with abundant individual tracking data and studies describing their movements and habitat preference both in Norway and North America. Recent projects in the Gardermoen area (Roer et al. 2018a, Roer et al. 2018b) and ongoing studies in the broader Østfold-Akershus (Anna Melhoop, Christer Rolandsen, Bram van Moorter et al., in prep) are investigating habitat quality and habitat permeability for moose in the region that contains Ski municipality. This work provides an opportunity to model GI for this pilot project using habitat quality models and habitat permeability models with locally and recently derived parameter estimates—producing the most current and realistic assessment of GI for moose in Ski Municipality.

5.1.1 Moose habitat quality model

We modelled habitat quality by matching GPS tracking data with the landscape characteristics at those locations, using Resource Selection probability Functions. We used tracking data from 55 moose in Akershus county monitored from 2009 to 2013 with GPS collars (Roer et al. 2018a, Roer et al. 2018b). To reduce the potentially disproportionate impact of tracking data from a subset of animals that had long-lasting collars, we limited individuals' trajectories to a maximum duration of 2 years ($n=41$). We selected one location at random before and after noon each day, which yielded an average of 683 GPS locations per individual ($SD=392$; [min;max]:[113;1460]). We first reclassified land cover data from AR5 into 12 categories of relevance for moose (**Table 2**), generating an additional raster layer for stand age for all forest pixels. We then estimated the impact of infrastructure for each pixel by calculating the density of buildings from N50 within a 2500 m radius and the log-transformed distance to the closest roads (ELVeg), weighted by the road type (i.e. Europaveg, Fylkesveg, Kommuneveg, Privatveg, Skogsveg).

We used environmental data representing land cover and infrastructures, selected and pre-processed as described below, based upon ecological considerations. We first reclassified land cover data from AR5 into 12 categories of relevance for moose (**Table 2**), generating an additional raster layer for stand age for all forest pixels. We then calculated the density of buildings from N50 within a 2500 m radius and the log-transformed distance to the closest roads (ELVeg), weighted by the road type (i.e., Europaveg, Fylkesveg, Kommuneveg, Privatveg, Skogsveg). We used also road traffic data for Ski municipality provided by Statens Vegvesen.

Table 2. Land cover categories deemed relevant for estimating moose habitat quality (Norwegian category names in parentheses) and the AR5 land cover classifications they were generated from (right column).

Reclassified land cover category	AR5 Land cover classes
Agricultural areas (<i>Innmark</i>)	artype: 21, 22, 23
Open, non-marsh areas (<i>Åpen fastmark</i>)	artype: 50
Marsh/bog (<i>Myr</i>)	artype: 60
Water (<i>Vann</i>)	artype: 80, 81
Developed area (<i>Bebyggd areal</i>)	artype: 11
Transportation infrastructure (<i>Samferdsel</i>)	artype: 12
Highly productive conifer forest (<i>Høy bonitet barskog</i>)	artype: 30, artreslag 31, arskogbon 14,15
Moderately productive conifer forest (<i>Middels bonitet barskog</i>)	artype 30, artreslag 31, arskogbon 13
Minimally productive conifer forest (<i>Lav bonitet barskog</i>)	artype 30, artreslag 31, arskogbon 11, 12
Broadleaf forest (<i>Lauvskog</i>)	artype 30, artreslag 32
Mixed conifer-broadleaf forest (<i>Blandingskog</i>)	artype 30, artreslag 33
Not mapped (<i>Ikke kartlagt</i>)	artype: 99

We modelled habitat quality using Resource Selection Probability Functions using a matched used-available design (Panzacchi-van Moorter et al 2015). The model compares the landscape characteristics recorded at observed animal locations with characteristics recorded at available locations chosen randomly within the same study area. For each location used by moose, we sampled 5 locations randomly on a 100-meter grid inside the individual home range. The preliminary model results are shown below (**Table 3** and **Figure 12, left panel**; Anna Melhoop, Christer Rolandsen, Bram van Moorter et al, in prep).

By multiplying the parameter estimates from **Table 3** with the environmental characteristics (density of houses, distance to nearest road and its type, AR5, forest age) of each pixel, we obtain² the predicted probability of observing a moose in this pixel. We used the predicted probability of observing a moose as a proxy for habitat quality.

² More precisely, this multiplication provides us with the predicted value on the linear scale, which after applying the inverse of the logit-link function gives us the predicted probability.

Table 3. Parameter estimates (logit link) for the Resource Selection Probability Function model used to predict moose habitat quality in Ski Municipality. Note that the model results may not be final, as the work is in progress (Anna Melhoop, Christer Rolandsen, Bram van Moorter et al., in prep).

	Estimate	Std. Error	z value	Pr(> z)
Intercept	-2.7580048	0.3047818	-9.049	< 2e-16 ***
building_2500	0.0081721	0.0002942	27.781	< 2e-16 ***
log_road_dist	1.2317375	0.0445148	27.670	< 2e-16 ***
ar5_recoded0	-5.5750928	0.2393720	-23.290	< 2e-16 ***
ar5_recoded1	-3.9458351	0.1943662	-20.301	< 2e-16 ***
ar5_recoded2	-3.5329690	0.2001405	-17.652	< 2e-16 ***
ar5_recoded3	-2.8824821	0.1871843	-15.399	< 2e-16 ***
ar5_recoded5	-5.7820655	0.2968021	-19.481	< 2e-16 ***
ar5_recoded6	-3.2229161	0.2355395	- 13.683	< 2e-16 ***
ar5_recoded9	0.0526008	0.0147858	3.558	0.000374 ***
ar5_recoded10	0.3292635	0.0234613	14.034	< 2e-16 ***
ar5_recoded11	-0.6715858	0.0406834	- 16.508	< 2e-16 ***
ar5_recoded12	-0.2346668	0.0329300	-7.126	1.03e-12 ***
road_typeE	-1.7599436	0.3986670	-4.415	1.01e-05 ***
road_typeF	-0.6970963	0.1729427	-4.031	5.56e-05 ***
road_typeK	0.3210878	0.2025749	1.585	0.112959
road_typeS	1.5511954	0.1447047	10.720	< 2e-16 ***
log_forest_age	-1.4063869	0.1008370	-13.947	< 2e-16 ***
log_road_dist:road_typeE	0.9209756	0.1825086	5.046	4.51e-07 ***
log_road_dist:road_typeF	0.2564427	0.0746335	3.436	0.000590 ***
log_road_dist:road_typeK	-0.2990100	0.0897099	-3.333	0.000859 ***
log_road_dist:road_typeS	-0.6363915	0.0603166	-10.551	< 2e-16 ***

5.1.2 Moose Friction model

We modelled landscape friction to moose movements using the same GPS tracking data described above. The environmental data used were similar to those used for the habitat quality model, but they were pre-processed slightly differently because data required to quantify friction to movements need to be specifically selected to describe the ability to traverse environmental features, rather than habitat preferences.

For environmental covariates, we used AR5 land cover data together with SatSkog data on forest age to classify land cover into 6 categories: agricultural land, bog, developed areas, young forests, old forests, and water. The model inputs pertaining to infrastructure included data for buildings from N50, roads and railways from ELVeg, and road traffic levels of major roads in Ski Municipality from Statens Vegvesen (**Figure 10**). Finally, we included a terrain data for slope from Statens kartverk.

Data were prepared by measuring environmental features *along each moose step* (as opposed to the environmental features measured at the start and end point of each step as in the habitat quality model). Hence, we calculated the *proportion* of the different land cover class traversed by each step, the maximum slope encountered along a step, whether a step crossed a railway or road with different traffic loads, whether a step would bring the animal closer or further to the closest building (a log-transformed distance to the nearest buildings) or to the closest road (log-transformed distance to the nearest road). The model also accounted for the length of each moose step.

We used a Step Selection Probability Function (SSPF) originally developed for reindeer but adapted to moose tracking data in the area surrounding the Gardermoen airport (Roer et al. 2018a, Roer et al. 2018b). The model compares the landscape features traversed by each individual moose at each step (i.e. two consecutive GPS locations, separated by 2 hours), to those the same individual could have traversed if it took a similar step in a different direction (**Figure 5**). The model then calculates the probability of crossing each landscape feature based on all comparisons between observed and alternative movement options.

The resulting habitat friction map, predicted for Ski Municipality using parameters from the SSPF, is shown in **Figure 11, right panel**. The friction map shows that urban areas, areas with high traffic and a dense network of infrastructures present the highest friction to moose movements.

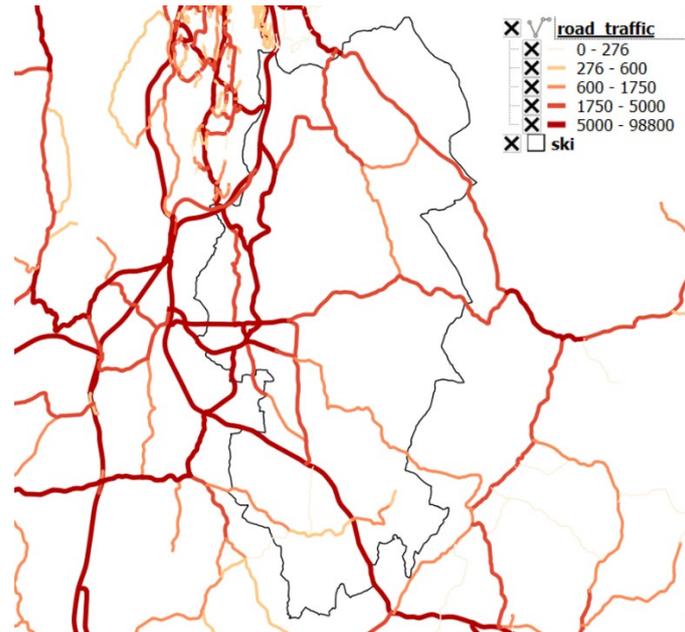


Figure 10. Road traffic data in Ski municipality provided by Statens Vegvesen, with traffic levels expressed as the mean automotive usage per day, averaged over an entire year (“årsdøgntrafikk”). We used these data as an input layer for the moose friction model, because moose are less likely to traverse highly used roadways.

5.1.3 GI for moose

The GI model for moose follows the protocol we described in Chapters 2.3 and 3.4. The ecological question for models in this pilot project was to identify **habitat connectivity for the all three species’ home range**, i.e. for “normal activities of food gathering, mating, and caring for young” (Burt 1943) in Ski Municipality. This goal determined the spatial extent for the analyses and model parameters we chose. Our data and literature indicate that most daily activities for moose occur approximately within a 5 km radius, so we selected this value to describe the maximum movement distance to be considered in this project. If we had been interested in modelling GI for moose dispersal and range expansion, however, we would have chosen a much larger maximum distance (possibly around 100 km), which would have led to using a larger spatial extent for the analyses and would have likely led to different GI maps.

We used a wider spatial extent (19 x 27 km) for moose than for bumblebees and forest insects (15 x 27 km) to account for moose’s larger spatial requirements to avoid possible edge effects. We also used a larger pixel resolution (200 m) to speed up computation of this larger number of pixels. We compare the result of computations performed at the standard spatial extent for the

Ski study area, and at the larger spatial extent in Chapter 6.3; a larger spatial extent in this case is advisable to avoid edge effects.

After exploring a range of values, we selected a Θ value of 0.01 for the RSP algorithm, resulting in a reasonable trade-off between the Least Cost Path and all possible random paths in the landscape. Note that, to date, there is no objective approach for to automatically identifying the best Θ value. However, using any intermediate Θ value provides a better alternative to both using extreme values (representing LCP and RW), as it allows avoiding the pitfalls associated with either extremes. Other technical details for the moose model can be found in Appendix 1. Each of the models described above (on an area of ca. 19 x 27 km, 200 m pixel resolution) needed about 2 hours to run. (but note that the code can be optimized for faster computation).

The *Habitat Functionality* map for moose (**Figure 12, left panel**) illustrates the distribution of well-connected high-quality moose habitat within the study area. Dark green pixels denote the areas that have the greatest functionality, or that are expected to be used by more moose in Ski municipality. The right panel of **Figure 12** illustrates the *Movement Flow* metric. Here dark green pixels represent areas that can serve as the most popular movement corridors, or where a high movement flow of moose is expected.

The side-by-side comparison of the distributions of *Habitat Functionality* and *Movement Flow* metrics for moose in Ski can help illustrate what each metric captures and the relationship between the two. The areas with high *Habitat Functionality* values represent important habitat for moose (a.k.a. “core areas”), because they are both high quality and well connected to other areas of high quality. The areas with high *Movement Flow* values are important for movement that might connect clusters of important moose habitat. If changes in land use were to decrease movement flow of an area, it could affect the functionality of the habitat in its proximity. For example, the construction of a linear barrier such as a fence or a highway that isolates an area with high functionality from other high-quality habitat would decrease the area’s functionality. To maintain (or enhance) GI for a focal species or species group, the landscape needs to retain both areas with high *Habitat Functionality* values and areas with high *Movement Flow* values.

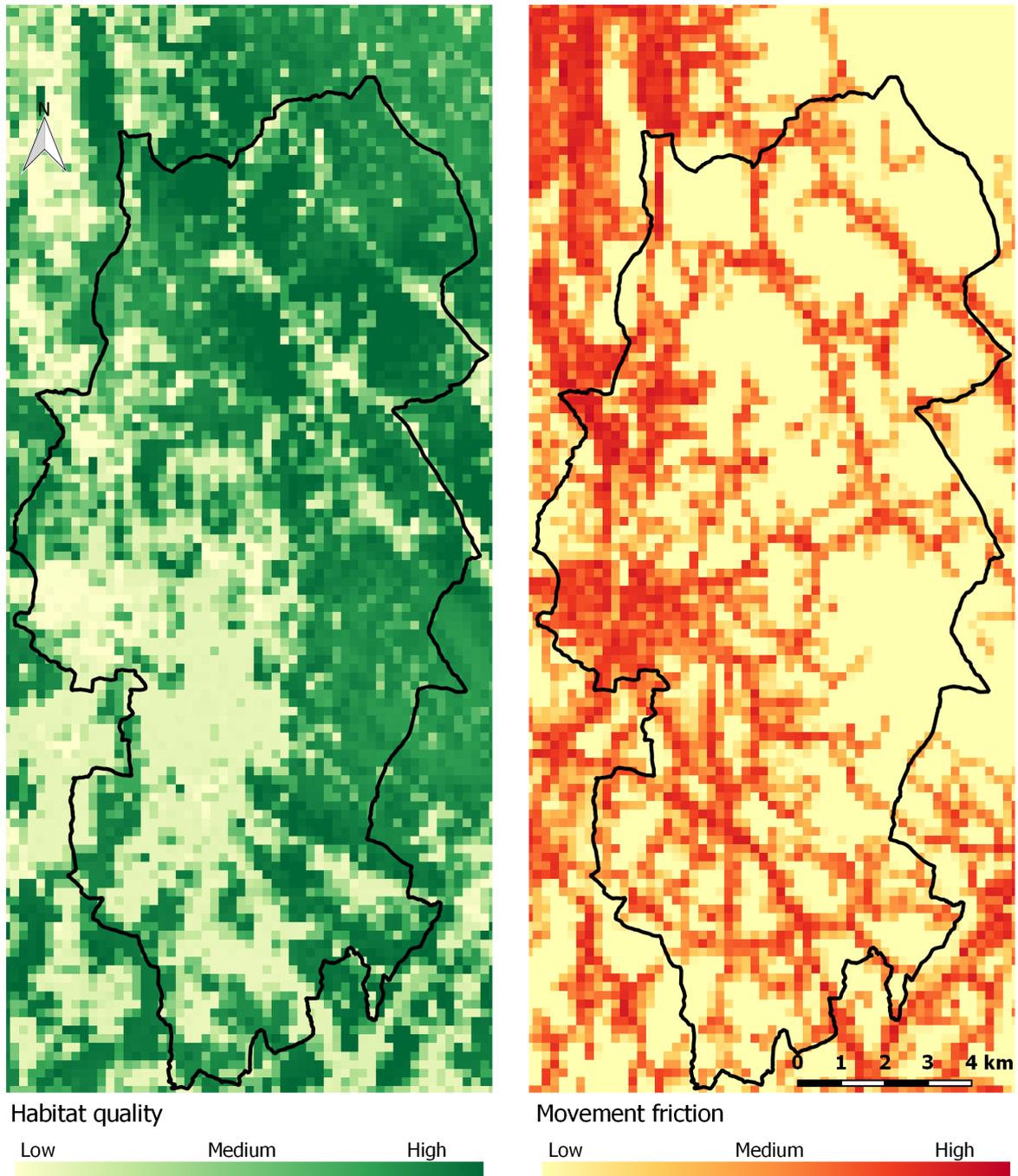


Figure 11. Habitat quality/ preference (left) and movement friction (right) input layers for modelling GI for moose in Ski municipality.

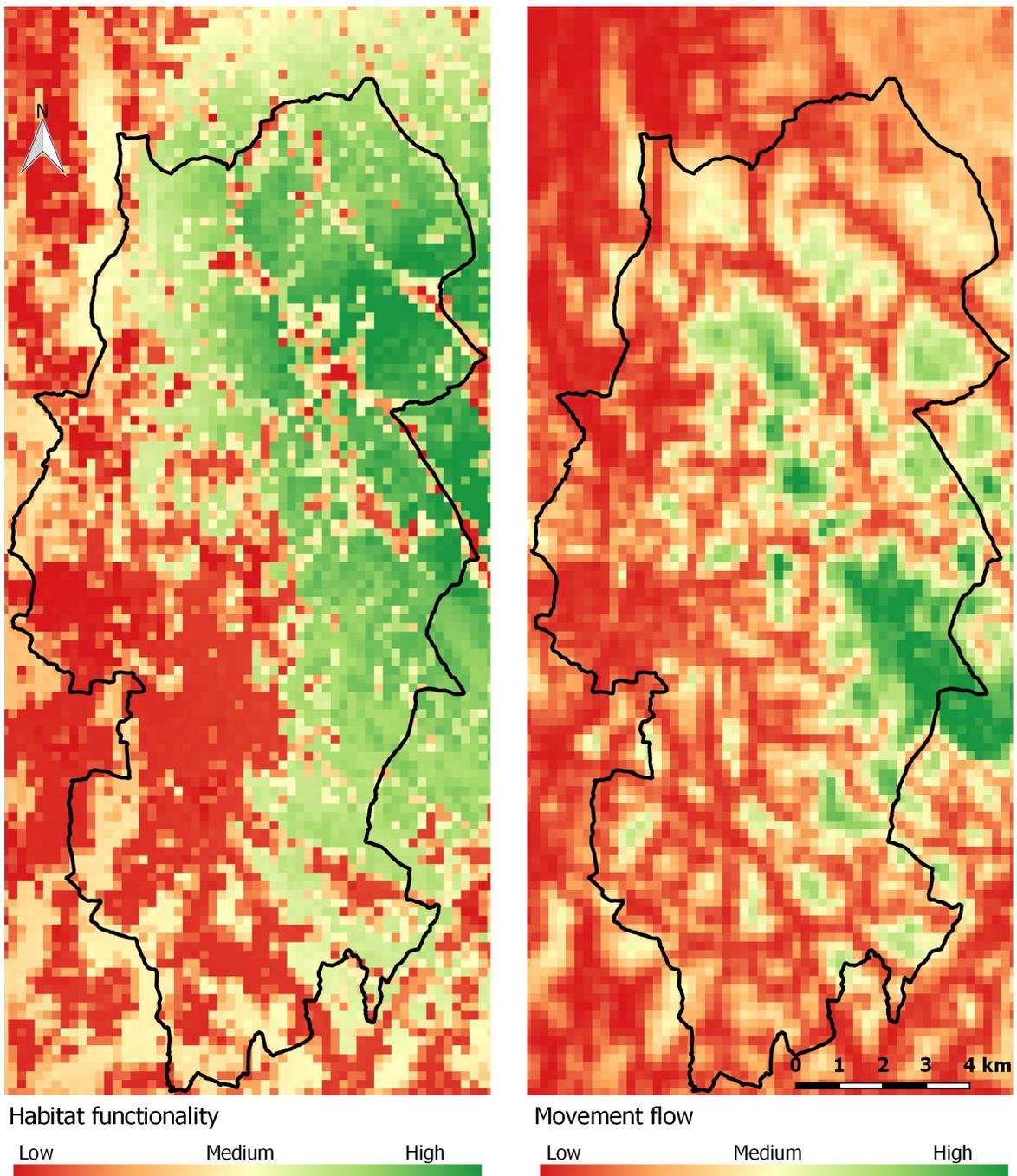


Figure 12. Green infrastructure for moose in Ski municipality, modelled with a 200 x 200 meter grid in an area larger than the one visualized in here for the purpose of avoiding edge effects (see **Figure 18**, chapter 6.3 for further explanation). *Habitat functionality* (left) depicts the locations of important habitat for moose persistence because it is both of high quality and well connected; dark green areas indicate areas where a higher moose abundance is expected, due to combined higher quality and accessibility. *Movement flow* (right) depicts important movement corridors ensuring access to high quality habitat. Darker green areas illustrate areas where a higher flow of individual moose is expected.

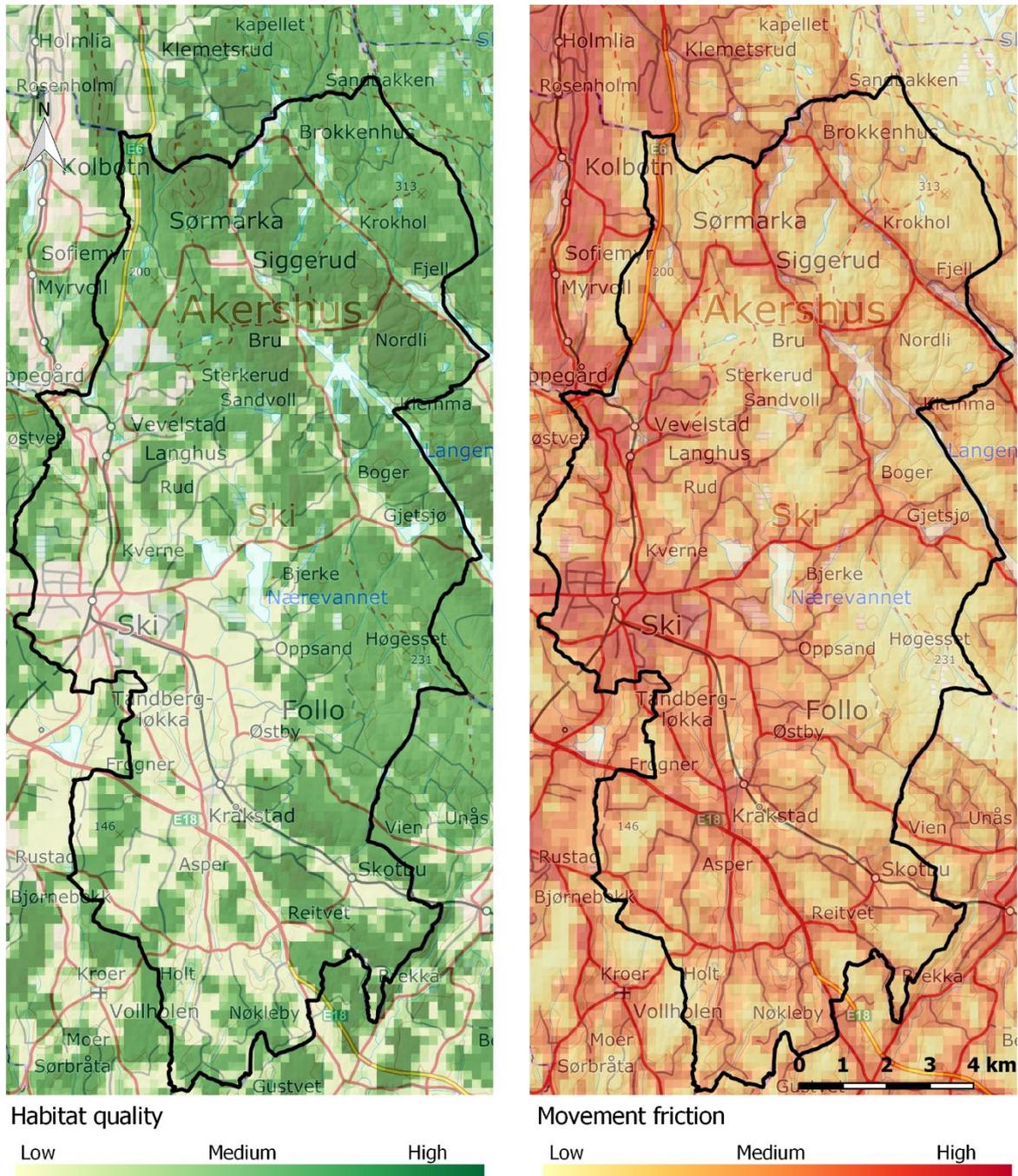


Figure 13. Habitat quality/ preference (left) and movement friction (right) input layers for modelling GI for moose in Ski municipality, superimposed upon a Topografisk Norgeskart (Norwegian Mapping Authority).

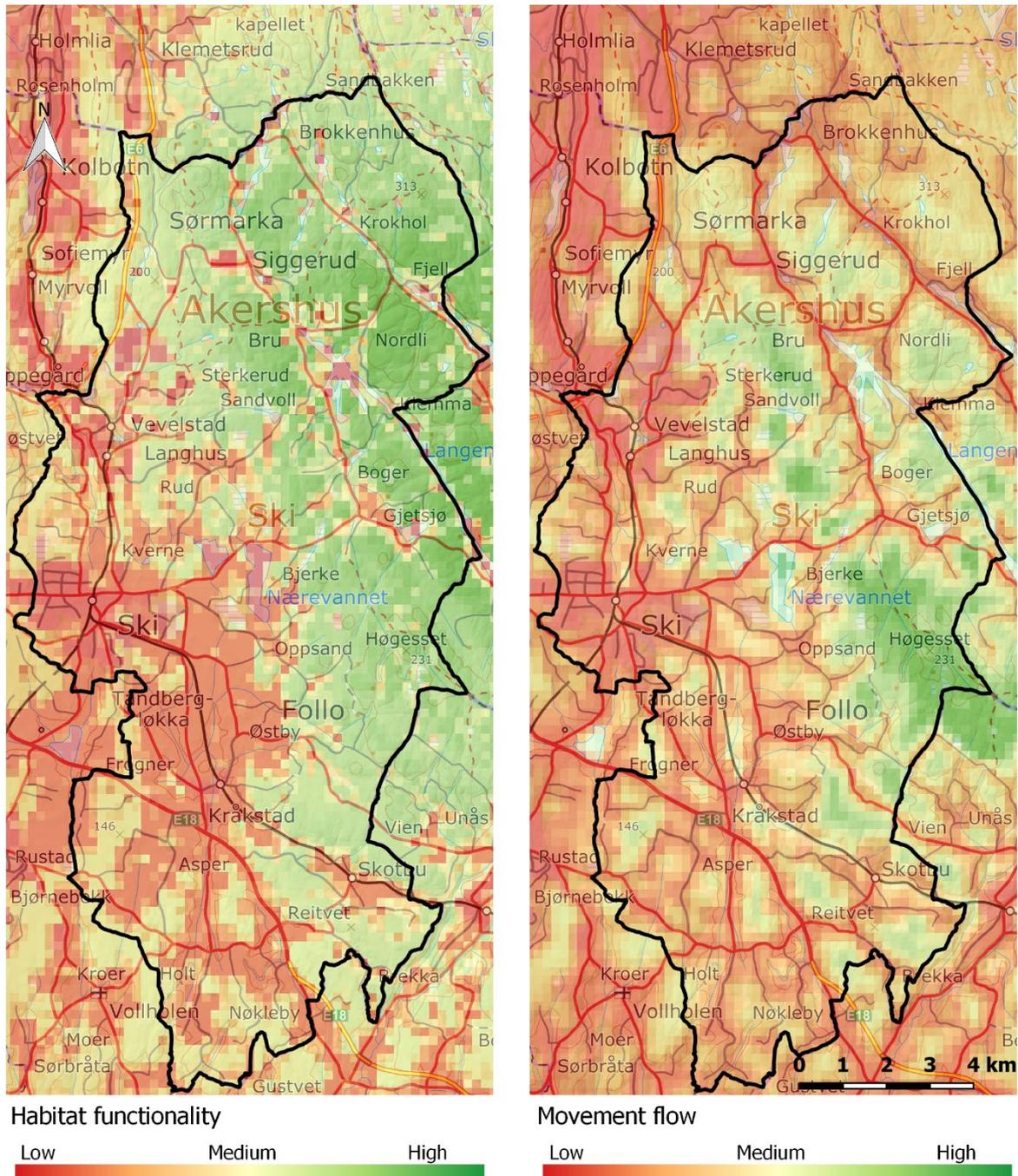


Figure 14. Green infrastructure for moose in Ski municipality (see figure 12), superimposed upon Topografisk Norgeskart (Norwegian Mapping Authority).

5.2 Winged forest insects associated with old conifer forests

Our second set of GI model addresses the movement needs for a loosely-defined group of winged forest insects associated with older conifer forests. Whereas the moose model assess GI for a single species with a considerable amount of GPS tracking data available for parameterizing area use patterns, this forest-insect model provides an example of a GI assessment whose surrogate consists of a dispersal guild, or a group of organisms that have similar fine-scale movement behaviour (Lechner et al. 2017), and for which most information are based upon literature and expert assessments.

We defined the dispersal guild for this model as a group comprised of winged insects that perform best in old growth conifer forests, but with limited dispersal abilities (i.e., not exceeding 2 km flight). This group would include the many species of saproxylic insects (insects that depend on dead and decaying wood) as well as the species whose habitat quality will increase with forest age (i.e. insects who either feed on or live in forest fungi that grow in these environments). This group includes many red-listed species of beetles, flies, moth/butterflies, and countless other insect families of conservation concern. This example is a very simple GI model whose purpose is to illustrate the modelling process for a broadly-defined species group and using expert assessments. It is not intended to provide a basis for any forest conservation planning. For that we would want to use a more precise definition of the species group and a more systematic collection of expert assessments that would have exceeded the scope of this project.

5.2.1 Forest insect habitat quality model

We generated a deterministic habitat quality model by using expert assessments of the relationship between insect presence and land cover. We focussed on forest composition and stand age, based on joint information from the AR5 and SatSkog datasets, and we grouped all other AR5 categories. We consulted several NINA researchers who are specialists in forest entomology and asked them to identify how information from nationally available data sources (i.e., SatSkog information might relate to variation in habitat quality for this dispersal guild. These entomology experts maintain that habitat quality is a non-linear function of stand age (**Table 4**), and that young forests often contain enough dead and decaying wood from the preceding harvest to provide a better access to resources than forests of an intermediate age. Forest with the highest habitat quality included all forest areas designated as special conservation areas (i.e., *Verneområder*), and those with documented attributes important for biodiversity (i.e., *MiS figures*), based on the Naturbase and SatSkog data sources. We expressed habitat quality with a relative metric, scaled from 0 to 1.

Table 4. Expert-based input parameters for models of habitat quality and landscape friction for a dispersal guild consisting of winged forest insects associated with older conifer forests.

Land cover category	Habitat quality	Friction	Source
< 10 years	0.4	0.2	SatSkog
10 - 25 years	0.2	1	SatSkog
25 - 40 years	0.3	1	SatSkog
40 - 60 years	0.6	0.5	SatSkog
60 – 80 years	0.8	0.5	SatSkog
>80 years; conservation areas; MiS-figures etc.	1	0.5	SatSkog/ Naturbase
Sea	0	1	AR5
All other non-forest categories	0	0.5	AR5

5.2.2 Forest insect friction model

We generated a deterministic landscape friction input layer from forest entomology experts, using the same forest classification typology as the habitat model (**Table 4**). We expressed landscape friction as a relative value scaled between 0 and 1. Experts reasoned that young forests would provide the least friction to movement because individuals would move more freely in thinner stands, as well as detect potential high-quality resource patches more easily than in dense growth. Intermediate age stands and non-forest land cover have the highest friction. Experts reasoned that individuals are comparatively less likely to pass through intermediate age forests because these areas will generally feature lower availability of suitable substrates. The dense tree growth that characterizes the structure of even-age forests of these ages also constitutes a physical barrier that hinders flight and diffusion of chemical signals that can signal the location of suitable host trees.

5.2.3 Modelling GI for forest insects

Using the protocol we describe earlier (Chapters 2.3 and 3.4), we produced the two centrality metrics: *Habitat Functionality* and *Movement Flow*, at a 100 x 100 m resolution. The Habitat Functionality metric map for forest insects (**Figure 16, left panel**) illustrates the distribution of well-connected high-quality habitat within the study area. Dark green pixels denote the areas that have the greatest functionality for persistence of forest insects with habitat requirements tied to older forests in Ski municipality. The right panel of **Figure 16** illustrates the Movement Flow metric. Here dark green pixels represent areas that can serve as likely movement corridors, or where a movement flow of these insect species would be greatest.

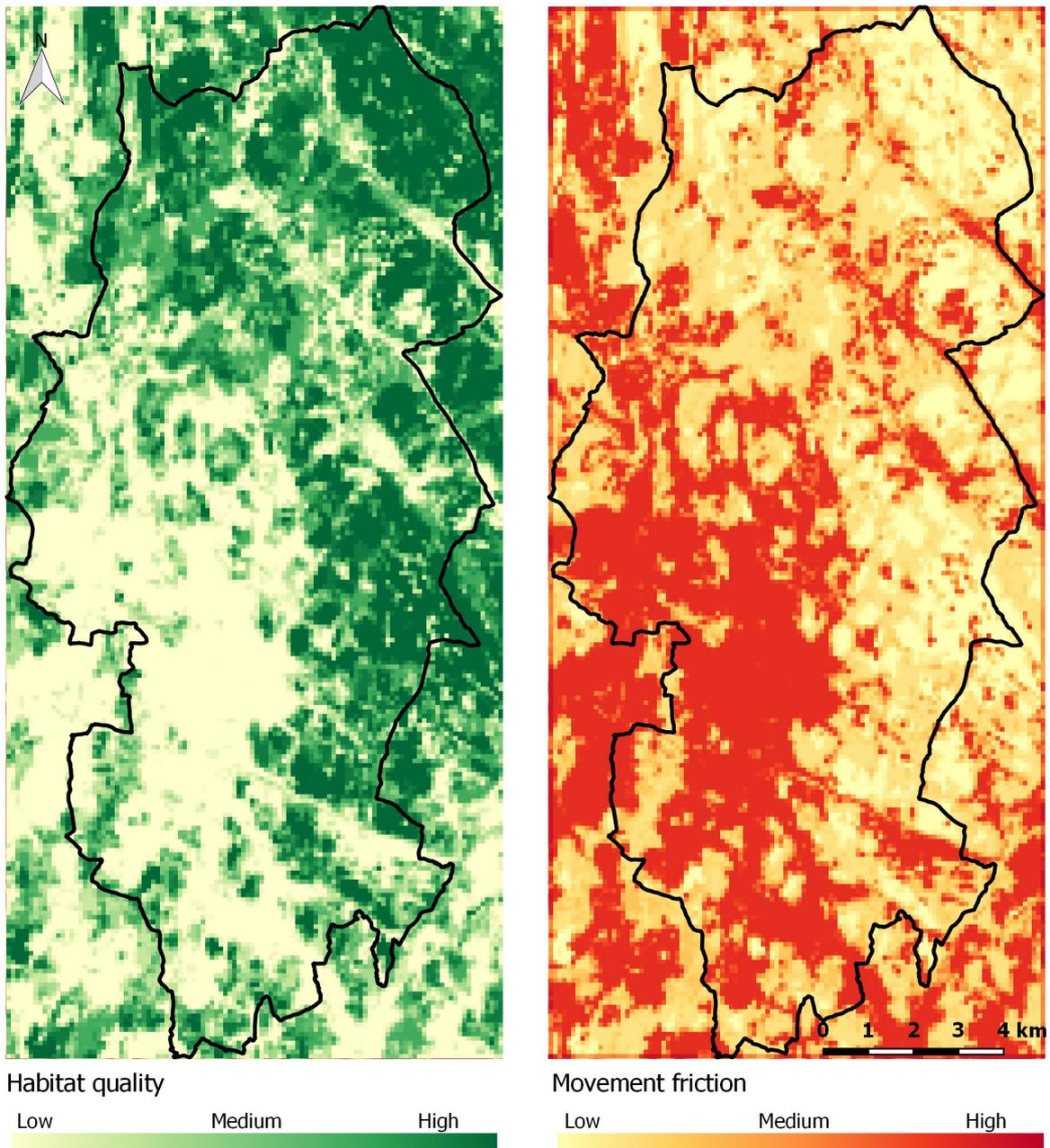


Figure 15. Habitat quality (left) and movement friction (right) input layers for modelling GI for forest insects in Ski municipality.

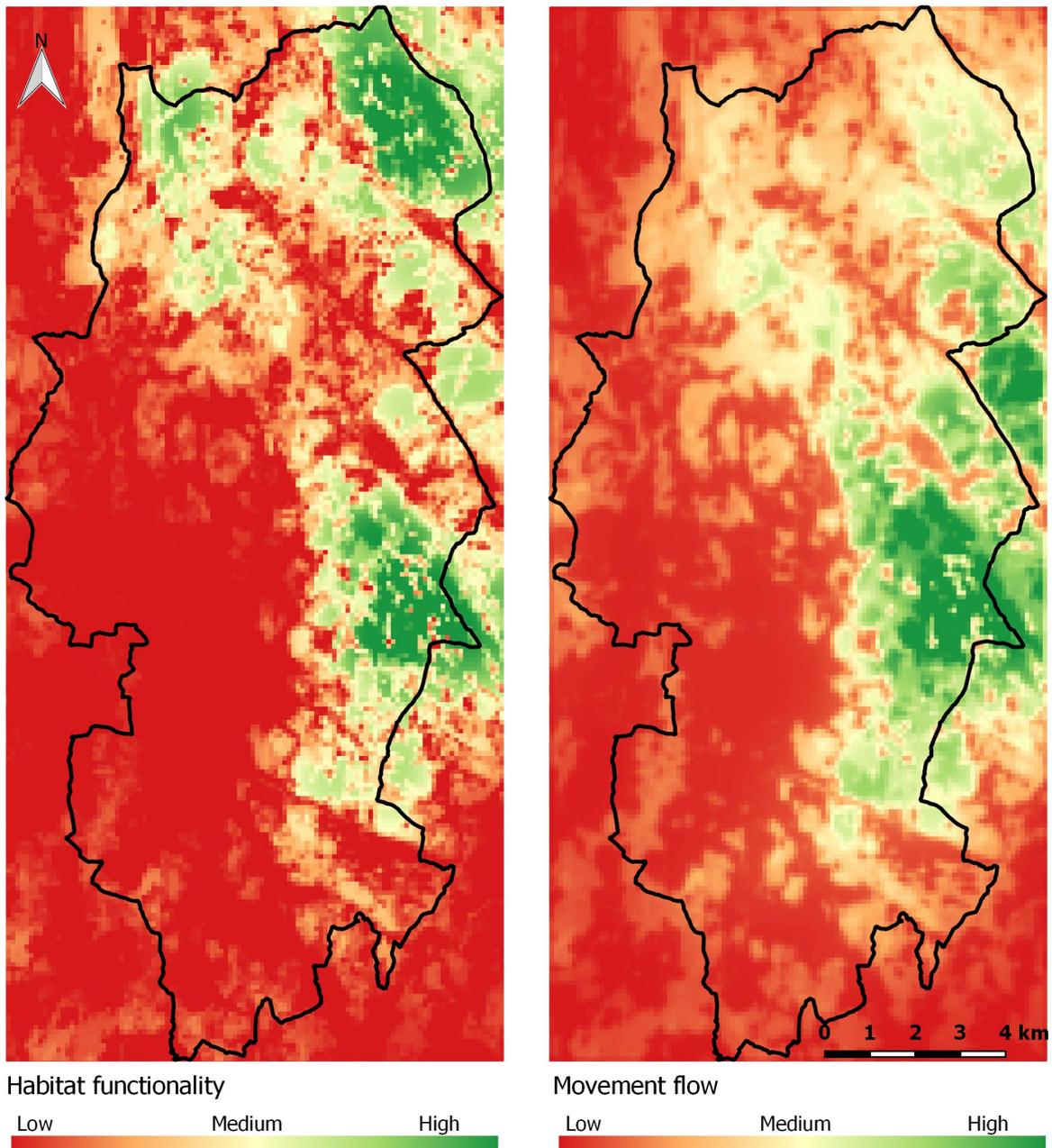


Figure 16. Green infrastructure important to forest insects living in older forest growth, modelled for Ski municipality and its surrounding areas with a 100 x 100 m grid. Habitat functionality (left) depicts the locations of important habitat for forest insects' persistence because it is both high quality and well connected. Movement flow (right) depicts the areas that are important for mobility, or the locations of potential corridors that connect high quality habitat.

5.3 Bumblebees

We developed the third GI model using bumblebees (*Bombus* spp.) as the model object. Animal-mediated pollination is both an integral ecosystem process and a key ecosystem service (ES). With an estimated 87 % of all flowering plant species depending on insect pollinators for sexual reproduction (Abrol 2012, Ollerton et al. 2011), pollinator-plant relationships may be one of the most ecologically important animal-plant interactions (Kearns et al. 1998). Reports documenting global declines among all key insect pollinator groups—including honeybees, bumblebees and solitary bees—are therefore a source of great concern (Bartomeus et al. 2013, Goulson et al. 2008, Potts et al. 2010).

Because bumblebees represent a group comprised of numerous species (there are 35 known species of *Bombus* living in Norway) with comparable body sizes and dispersal flight capacities, this model also essentially uses a dispersal guild approach. Species of bumblebees found in Norway certainly differ in their habitat requirements and the flowering plants they prefer to forage amongst. However, in contrast to the forest insect model, bumblebees generally represent a more homogenous group with more similar habitat preferences and resource use. Accordingly, this model attempts to incorporate greater detail in the landscape factors that determine habitat quality. It does this by using data sources that can capture heterogeneity in land cover that is relevant for insects that generally do not travel long distances. The model uses parameter estimates provided by expert evaluations. However, investigators also used field observations to validate the model. This data lead to re-evaluating the model design and modifying the parameter estimates.

5.3.1 Bumblebee habitat quality

We modelled habitat suitability for bumblebees using parameters from the ESTIMAP model describing habitat suitability for pollinating insects in the Oslo municipality (Stange et al. 2017). This model for Oslo is a modified version of the original ESTIMAP model for pollinator potential, which was originally developed for assessment at the continental scale (Zulian et al. 2013a, Zulian et al. 2013b). The Oslo model uses AR5 data, reclassifying polygons into 60 land cover categories—including 30 different forest types—based on relevance to pollinating insects (Table 4). ESTIMAP uses a forest classification that consists of six broader categories based on expert assessments of the forest attributes that pertain to pollinating insects' life histories. Forest classification was based on categories of dominant tree variety and the growth potential (impediment, low, medium high and very high), while additionally differentiating between core and edge habitat. The model development involved conferring with several experts familiar with local pollinating insect taxa through an iterative process to arrive at consensus values for land cover that express categories' relative *habitat suitability* (i.e., quality) for the pollinating bee species occurring in Oslo. Land cover categories that are incapable of providing either floral resources or nesting sites (e.g., water surfaces or densely built areas) were valued at or near zero. Land cover categories that represent the best possible habitat within the study area were valued at 1. Habitat suitability values also attempted to capture variation in the temporal availability of floral resources, such that only land cover categories expected to offer the most continuous availability of floral resources received full habitat suitability value (1).

Preliminary validation analyses from insect sampling using pan traps indicated that the AR5 spatial dataset often failed to capture the heterogeneity in vegetation cover that investigators found in field observations for many of the land cover categories. They therefore applied imagery from the Sentinel 2 satellite (at 10 m resolution) to improve the detail of the information in the land cover classes from the AR5 land cover data. Sentinel 2 data includes 13 spectral bands, plus Normalized Difference Vegetation Index (NDVI). They used a Random Forest classifier in R Studio (RStudio Team 2016), based on 10 000 training points, to classify the imagery into five land cover classes. These classes included 1) Agriculture (low uniform vegetation that may include

mowed grass); 2) low (non-tree) vegetation; 3) tree canopy; 4) built-up infrastructure (buildings, roads and other artificial surfaces) and 5) water. The method achieved an 86 % classification accuracy. They then designated value adjustments for each combination of municipal and Sentinel 2 land cover categories (**Table 5**), consulting with experts to verify these value adjustments, and recalculated the ESTIMAP pollination model at a 10 x 10 m resolution.

Roadside vegetation often includes high densities of flowering plants, including many species that are popular among pollinators. Yet vehicle exhaust can disrupt bees' ability to detect floral odors (Girling et al. 2013), pollination rates can decrease as traffic speeds increase (Dargas et al. 2016), and collisions with vehicles may lead to increased bee mortality (Kallioniemi et al. 2017). Stange et al. (2017) therefore attempted to capture the detrimental effects that greater levels of automotive traffic could presumably have on pollinator foraging by generating a value-reduction layer based on the cells' proximity to aboveground, high-traffic roads (defined as Motorways, Freeways and Major roads in the TeleAtlas® MultiNet™ dataset 2013). They used an exponential decay function, with habitat suitability values reduced by 0.2 immediately adjacent to high traffic roads, and the effect diminishing to zero at 200 m distances from road edges. In more recent versions of the ESTIMAP model, which expanded the spatial extent to include the Ski municipality, these investigators concluded that they did not have enough empirical support for this approach. Moreover, land cover categories might adequately capture variation in habitat suitability and make a traffic element unnecessary. For the pilot project, we chose to use this simpler model as the input for habitat quality.

Table 5. Habitat quality and friction parameters for modelling GI for bumblebees. Columns S1-5 denote habitat quality parameter adjustments for pixels based on inputs from Sentinel 2 satellite imagery. (S1 = agriculture, S2 = non-tree vegetation, S3 = built, S4 = tree, S5 = water)

land cover class	Quality	friction	S1	S2	S3	S4	S5
Built-up	0.4	0.8	0.2	0.3	-0.3	0.2	0.05
Transportation	0.2	0.5	0.3	0.6	-0.1	0.3	0.05
Arable land	0.4	0	0.2	0.3	-0.2	0.2	0.05
Cultivated land	0.3	0	0	0.3	-0.2	0.2	0.05
Cultivated pastures coniferous	0.3	0	0	0.4	-0.2	0	0.05
Cultivated pastures deciduous	0.3	0	0	0.4	-0.2	0	0.05
Cultivated pastures mixed	0.3	0	0	0.4	-0.2	0	0.05
Cultivated pastures not forested	0.3	0	0	0.4	-0.2	0	0.05
Cultivated pastures	0.6	0	0	0.1	-0.5	0	0.05
Forest impediment coniferous, edge	0.3	0.8	0.1	0.4	-0.2	0	0.05
Forest impediment coniferous, core	0.2	1	0.1	0.4	-0.1	0	0.05
Forest impediment deciduous, edge	0.7	0.6	0	0.2	-0.6	0	0.05
Forest impediment deciduous, core	0.4	0.8	0	0.2	-0.3	0	0.05
Forest impediment mixed, edge	0.6	0.6	0	0.4	-0.5	0	0.05
Forest impediment mixed, core	0.25	0.8	0	0.4	-0.15	0	0.05
Forest low coniferous, edge	0.3	0.8	0	0.4	-0.2	0	0.05
Forest low coniferous, core	0.2	1	0	0.4	-0.1	0	0.05
Forest low deciduous, edge	0.7	0.6	0	0.2	-0.6	0	0.05
Forest low deciduous, core	0.4	1	0	0.2	-0.3	0	0.05
Forest low mixed, edge	0.6	0.6	0	0.3	-0.5	0	0.05
Forest low mixed, core	0.25	1	0	0.4	-0.15	0	0.05
Forest medium coniferous, edge	0.4	0.8	0	0.3	-0.3	0	0.05

Forest medium coniferous, core	0.3	1	0	0.4	-0.2	0	0.05
Forest medium deciduous, edge	0.8	0.6	0	0.1	-0.7	0	0.05
Forest medium deciduous, core	0.5	0.8	0	0.3	-0.4	0	0.05
Forest medium mixed, edge	0.8	0.8	0	0.1	-0.7	0	0.05
Forest medium mixed, core	0.4	1	0	0.4	-0.3	0	0.05
Forest high coniferous, edge	0.7	0.8	0	0.1	-0.6	0	0.05
Forest high coniferous, core	0.3	1	0	0.4	-0.2	0	0.05
Forest high deciduous, edge	0.8	0.6	0	0.2	-0.7	0	0.05
Forest high deciduous, core	0.6	0.8	0	0.2	-0.5	0	0.05
Forest high mixed, edge	0.6	0.6	0.1	0.3	-0.1	0	0.05
Forest high mixed, core	0.25	0.8	0.1	0.4	-0.15	0	0.05
Forest very high coniferous, edge	0.5	0.8	0.1	0.4	-0.4	0	0.05
Forest very high coniferous, core	0.2	1	0.1	0.4	-0.1	0	0.05
Forest very high deciduous, edge	0.9	0.6	0.1	0.1	-0.6	0	0.05
Forest very high deciduous, core	0.4	0.8	0.1	0.4	-0.3	0	0.05
Forest very high mixed, edge	0.75	0.6	0.1	0.15	-0.65	0	0.05
Forest very high mixed, core	0.25	0.8	0.1	0.4	-0.15	0	0.05
Open land / soil impediment not forested	1	0	-0.4	0	-0.9	-0.4	0.05
Open land / soil medium not forested	1	0	-0.4	0	-0.9	-0.4	0.05
Open land / soil high not forested	1	0	-0.4	0	-0.9	-0.4	0.05
Open land / soil very high not forested	1	0	-0.4	0	-0.9	-0.4	0.05
Marsh impediment coniferous	0.1	0	0.3	0	0	0	0.05
Marsh impediment deciduous	0.1	0	0.3	0	0	0.3	0.05
Marsh medium mixed	0.1	0	0.3	0	0	0.2	0.05
Marsh high coniferous	0.1	0	0.3	0	0	0	0.05
Marsh high deciduous	0.1	0	0.3	0	0	0.2	0.05
Marsh high mixed	0.1	0	0.3	0	0	0.2	0.05
Marsh impediment mixed	0.1	0	0.3	0	0	0	0.05
Marsh impediment not forested	0.1	0	0.3	0	0	0	0.05
Marsh low coniferous	0.1	0.4	0.3	0	0	0	0.05
Marsh low deciduous	0.1	0.2	0.3	0	0	0	0.05
Marsh low mixed	0.1	0.3	0.3	0	0	0	0.05
Marsh medium coniferous	0.1	0.4	0.3	0	0	0	0.05
Marsh medium deciduous	0.1	0.2	0.3	0	0	0	0.05
Fresh water	0.05	0	0.3	0.4	0	0.4	0.05
Sea	0	0	0.3	0.4	0	0.4	0

5.3.2 Bumblebee friction model

We modelled landscape friction for bumblebees using the approach we used in the forest insects GI model. We used the same land cover categories as the habitat quality model and used expert assessments to indicate the likelihood that an individual would traverse a pixel for each land cover category. Bumblebees are winged insects and use olfactory cues to seek floral resources and their flight movements are generally not hampered by topography. The possible effects of other vertical barriers (buildings and vegetation) were accounted for by the land cover category scores.

5.3.3 Modelling GI for bumblebees

Using the protocol that we describe earlier (Chapters 2.3 and 3.4), we produced the two centrality metrics: *Habitat Functionality* and *Movement Flow*. The *Habitat Functionality* map for bumblebees (**Figure 18, left panel**) illustrates the distribution of well-connected high-quality habitat within the study area. Dark green pixels denote the areas that have the greatest functionality for persistence of lowland bumblebees in Ski municipality. The right panel of **Figure 18** illustrates the *Movement Flow*. Here dark green pixels represent areas that can serve as likely movement corridors, or where a movement flow of these insect species would be greatest. Like the two previous examples, we modelled GI for bumblebees at 100 x 100 m for processing feasibility. This resolution is coarser than that of the input layers for habitat quality and landscape friction, resulting in a loss of information that may be important for small bodied insects' short-distance foraging movements. Please see Chapter 6.3 for further discussion about the potential of modelling large extents at finer resolutions.

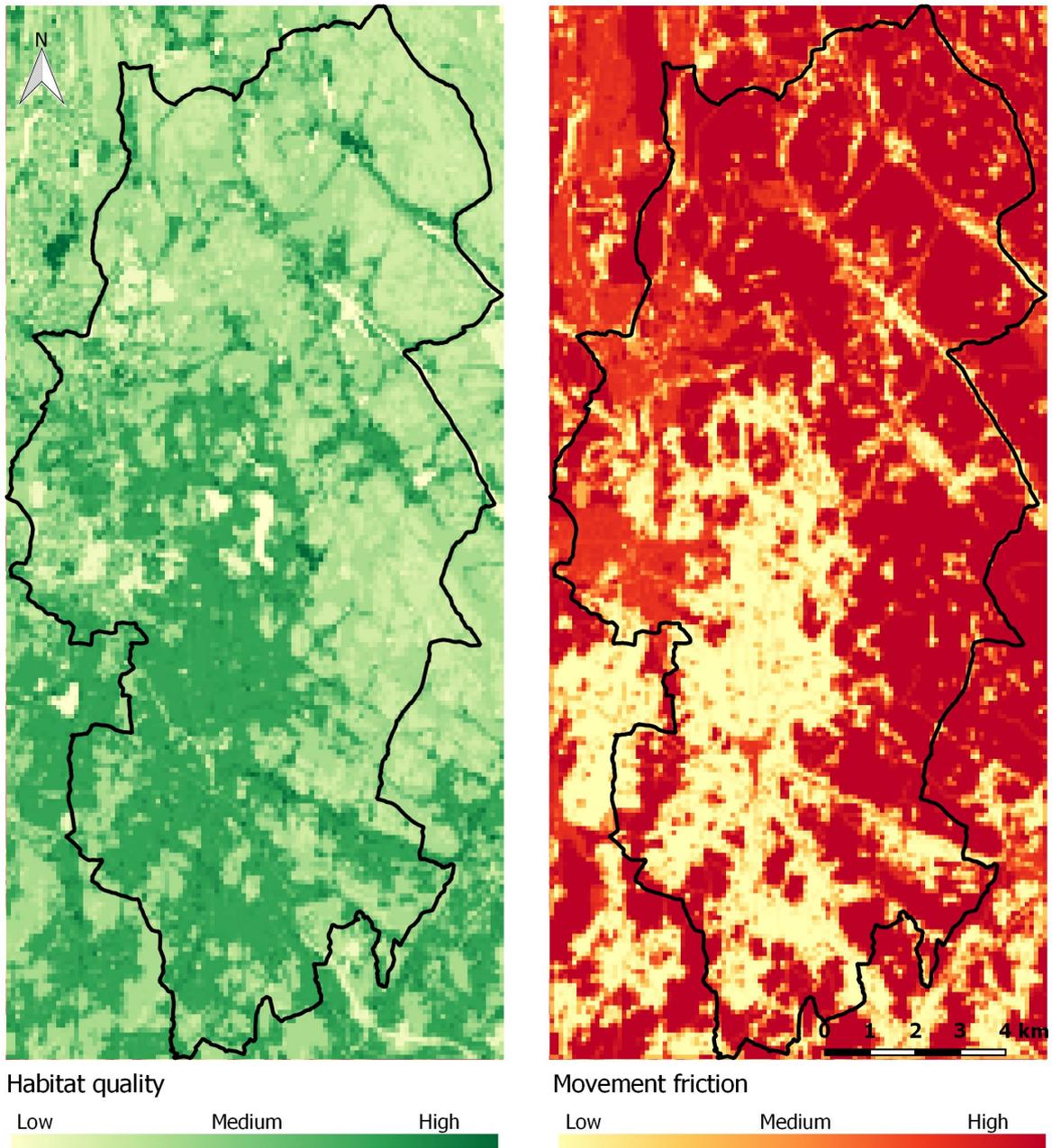


Figure 17. Habitat quality (left) and movement friction (right) input layers for modelling GI for bumblebees in Ski municipality.

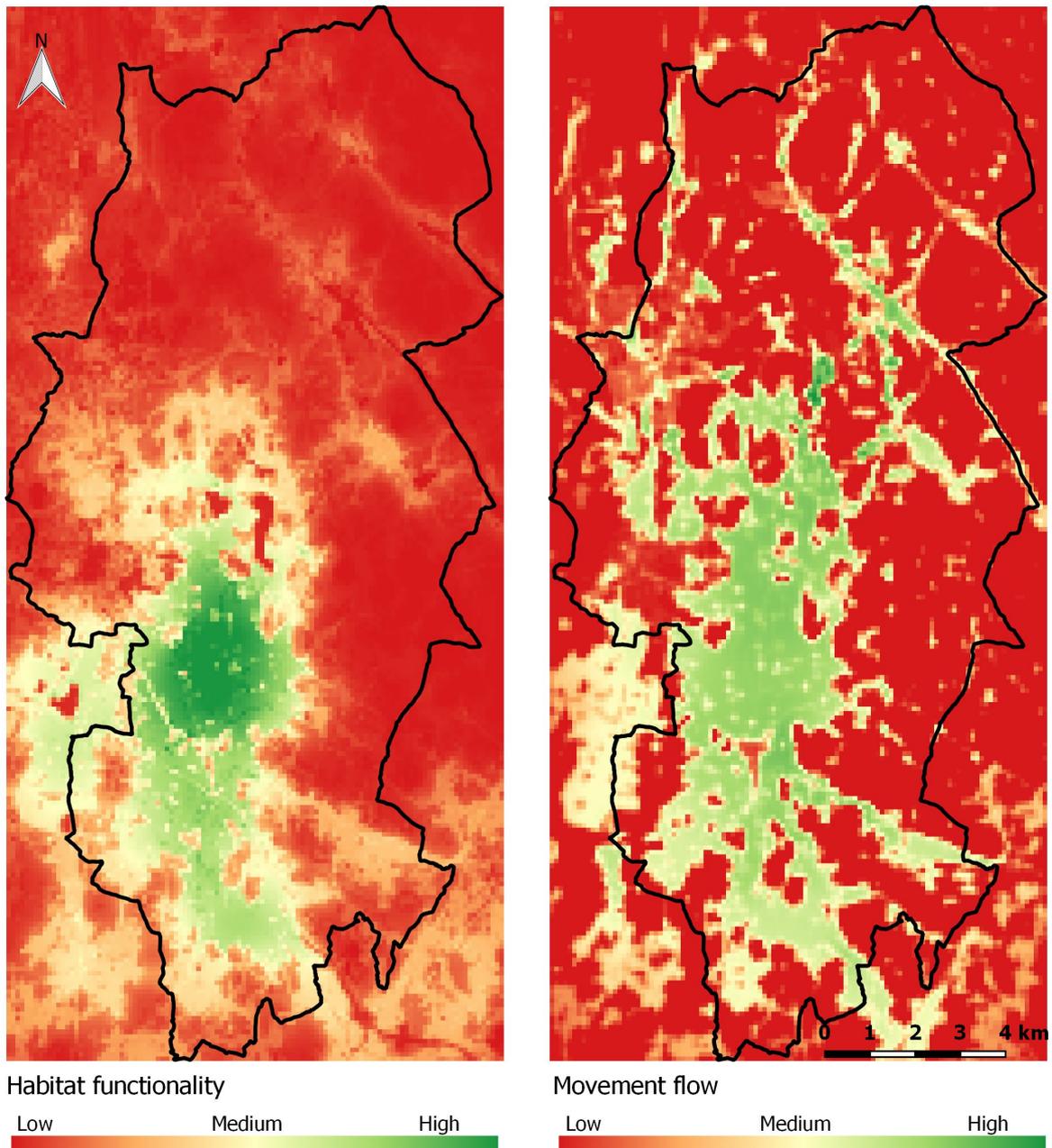


Figure 18. Green infrastructure important to most Norwegian bumblebee species, modelled for Ski municipality and its surrounding areas with a 100 x 100 m grid. Habitat functionality (left) depicts the locations of important habitat for the insects' persistence because it is both high quality and well connected. Movement flow (right) depicts the areas that are important for mobility, or the locations of potential corridors that connect high quality habitat.

6 Factors that can influence GI model outputs

6.1 Data quality

The outputs of any model are invariably determined by the quality and degree of uncertainty of the input data. Modelling GI requires **good quality, georeferenced, digital data on all environmental features relevant to describe the species' habitat preferences and landscape permeability**. If data on species (i.e. tracking data or observations) are not available, models can still be built using literature and expert assessments, but no estimate of accuracy can be provided. Each input model has a degree of uncertainty and we can expect that this uncertainty will propagate through the connectivity modelling process. When information on the species' habitat preference, permeability, and movement abilities are generated using data-driven models, we can quantify the uncertainty of our estimates with descriptive statistics. When model parameters come solely from expert-based assessments, the degree of uncertainty associated to these input data is unknown. It is therefore highly recommended to select data to minimize the error associated to the final estimates.

6.2 Model assumptions

The results of any model also reflect the conditions or assumptions built into it, and the question the model is intended to address. One of such assumptions refers to the parameter Θ used in the RSP algorithm (Kivimäki et al. 2014, Panzacchi et al. 2016, Saerens et al. 2009). A central step in GI assessment is the upscaling from a friction surface describing the local connectivity between adjacent pixels/areas to a network analysis to describe the connectivity between any pair of locations on the landscape (**Figure 4**). The choice of movement mode is therefore a central assumption in such assessments. A Least-Cost Path (LCP) represents one extreme of completely optimal movement, which requires the individuals to have perfect knowledge of the landscape and choose the most optimal path between a pair of locations, ignoring all other possible paths. The other extreme is random walk (RW) movement, which considers all possible paths between a pair of locations.

The user should be aware that there is always a choice of movement mode, typically LCP or RW, although the choice is often made unconsciously through the choice of software. There has been no comprehensive assessment of confidence intervals on GI. However, there has been several assessments of sensitivity of the components of the modelling framework. For example, Avon and Bergès (2016) used the PC in combination with LCP and RW approaches to identify prioritization areas for connectivity, and found that the choice of the algorithm (LCP vs RW) leads to very different prioritization recommendations. The Randomized Shortest Path approach that we advocate using interpolates the continuum between both extremes through adjustments of the parameter Θ (**Figure 6**). We argue that an intermediate value of Θ will consistently provide a more realistic depiction of connectivity, rather than just path (as in LCP), or all paths (as in RW). However, the RSP algorithm is under active development, especially in its use in movement ecology, and to date there are no established rules for selecting the degree of randomness or optimality in individuals' movement. Panzacchi et al. (2016) used a double-validation procedure with GPS data to select the Θ value that best matched wild reindeer movements. In this report, we have relied on visual assessments of the resulting connectivity maps and used values of Θ that appear to correspond with intermediate values of randomness. This issue of movement mode has only relatively recently been realized in the GI research community, and it is presently an active field of research.

The other important assumption refers to the species' movement patterns, which needs to be identified based upon both the best available knowledge, and the project goals. In this pilot project, we aim at identifying habitat *connectivity for the species' home range, i.e. for "normal activities of food gathering, mating, and caring for young"* (Burt 1943). Based upon data and literature

we know that most daily activities occur approximately within a 5 km radius for moose, and within a 2 km radius for beetles and pollinators (**Figure 19**). We illustrate here the scale of the movement patterns chosen for this project, using an exponential decay function, for moose, pollinators and beetles. This means that a moose would perform most of its activity within approximately a 5 km radius, although the animals could move farther than that, with a probability decreasing as distance from the starting point increases. It is important to note that if we had designed our model to address *connectivity for assessing the probability of colonization of new areas*, rather than connectivity for “normal” activities, we would have chosen larger values to represent these movements, based upon the maximum dispersal capabilities of the species. For moose, this might be up to 100 km. By changing this parameter, we might obtain very different connectivity maps at much larger spatial scales.

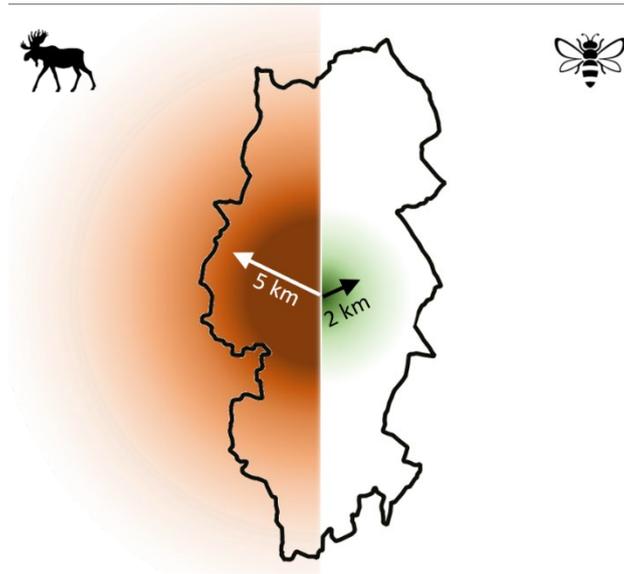
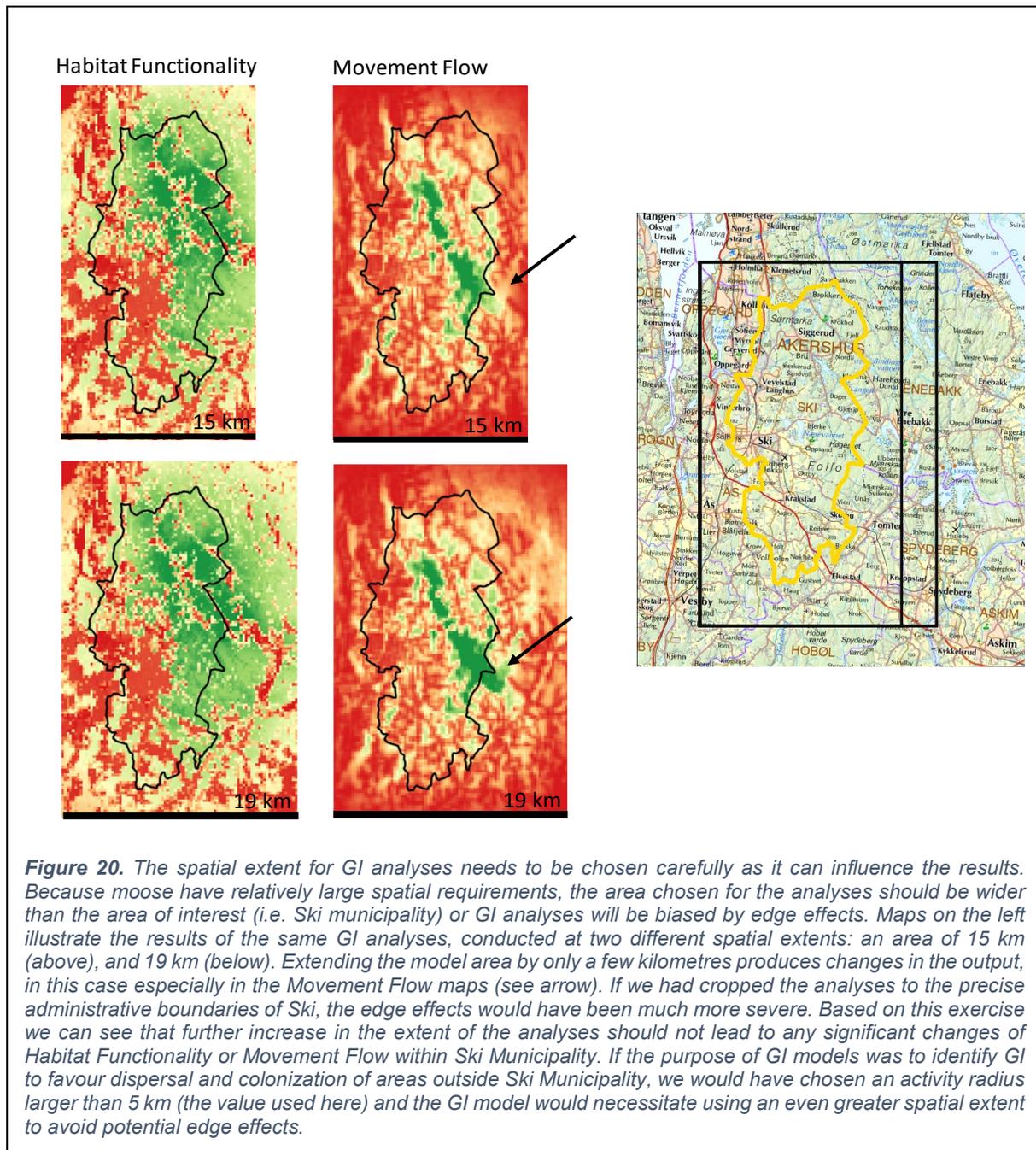


Figure 19. Model assumption: illustration of the scale of movement considered in this project for moose (5 km), forest-dwelling insects and pollinators (2 km), as compared to Ski municipality.

6.3 Spatial scale: extent and resolution

The spatial extent of an analysis plays an important role in the outcome of a connectivity analysis (**Figure 19**). Selecting an extent that is smaller than the range of a focal species can introduce edge effects to model outputs that can exclude areas with importance for the connectivity of species with larger dispersal abilities. On the other hand, the computational requirements set limits to the size of analysis' extent, particularly for high-resolution spatial data. Our group is working actively on optimizing the algorithms to make them even more efficient at computing GI metrics for very large areas, and we expect to make important advances on this front in the coming months. As a rule of thumb, one should increase the spatial extent of the analyses outside the focal area (e.g. municipality) to at least the same distance assumed as dispersal distance for the focal species to avoid edge effects (**Figure 20**).



There is also an important temporal component to determining what spatial extent will generate the most relevant descriptions of how GI will influence species persistence. In the context of climate change, we can expect that several species will need to shift their home ranges with respect to both latitude and elevation as individuals seek habitat that provides the best climatic conditions for survival, growth and reproduction. These shifts in species distributions will in most cases occur across several generations, particularly for species whose individuals have highly limited movement capabilities. Considerations related to range shifts, however, are generally addressed by regional land planning and may be of lesser importance for GI modelling at the municipal level.

The datasets for environmental attributes that we used as inputs for GI models (Chapter 4.2) all generally provide a spatial resolution that is appropriate and amenable for using the GI models in municipal planning contexts. As the development of the model for bumblebees demonstrated,

satellite imagery may be necessary to capture heterogeneity within the classification of land cover (at a 10 x 10 m resolution), especially for models of small-bodied insects with smaller home ranges and more limited dispersal capacities. It was too computationally demanding to model the entire extent of Ski municipality at a 10 x 10 m resolution within the short time frame of this pilot project. However, an adjustment of the code, already successfully tested, should allow for computation at much larger extents and much finer resolution.

6.4 Assessing and handling uncertainty

Uncertainty is an inherent aspect to any modelling exercise, and the history of connectivity assessment and management illustrates how vexing uncertainty can be with GI. Creating wildlife corridors was one of the earliest measures used to link populations that had become isolated as a result of human activities. Wildlife corridors proved to be an appealing conceptual option and attracted considerable investment in “green bridges”. Yet the knowledge base for the location and design of wildlife corridors consisted largely of either expert assessments or GIS approaches that lacked a capacity to address uncertainty. The hands-on initiatives and best-practice manuals for corridor design were developed in the absence of a sound theoretical framework to understand and model the underlying ecological mechanisms (Hess & Fischer 2001). Due to these shortcomings, designated wildlife corridors often failed to facilitate animal movements and did not guarantee population persistence (Gilbert-Norton et al. 2010).

Mechanistically-based models of species’ habitat preference and movement are a far better approach to assessing GI and evaluating management options, and they also provide options for addressing uncertainty in the analyses. We contend that the protocol we propose is among the most robust available in terms of limiting error propagation and handling uncertainty, but by no means does it eliminate uncertainty. Uncertainty is present in each of the numerous data layers required to build the models, it is inherent in the structure of each model, and it propagates at each step throughout the procedure. We can quantify part of this uncertainty, but it would be highly demanding to model the error propagation from input data through the long chain of modelling steps. Data-driven approaches provide the clearest estimates of uncertainty, and it is advisable to do these calculations. When model parameters come from expert opinions, the estimates of uncertainty are limited to the degree of agreement/disagreement among experts’ estimates and expert’s confidence in their own estimates. Accordingly, approaches that do not use data on species’ locations and identify corridors, barriers and core areas *a priori* have an inherent disadvantage as compared to data-driven and theoretically grounded statistical approaches. Strategies for reducing and accounting for uncertainty in the GI modelling procedure should:

- Use data-driven approaches whenever possible. They provide an objective basis for quantifying uncertainty and are generally a better option than expert opinion.
- Use input data for species and environmental variables that provides error estimates, which may be used to assess the robustness of the data themselves and potentially quantify error propagation through the procedure
- Quantify error and uncertainty associated with each step of the GI modelling procedure. For instance, the model coefficients of a habitat friction map may indicate that road permeability is 0.8. Such a coefficient is used to predict the friction map: every time there is a road in a landscape, the road is given the friction value of 0.8. However, parameter estimates are generated with an associated error (e.g., 0.8 ± 0.1). Using a bootstrapping procedure, it is possible to sample from the error distribution, and predict a series of friction maps in which roads are given a range of values randomly sampled from within the error distribution (i.e., between 0.7 to 0.9). This allows us to obtain several friction maps, with varying estimates for the friction effect of roads. By feeding a set of maps into the GI model, ideally for each of the parameters used, we can assess the robustness of the GI results with respect to the uncertainty of parameter estimates and obtain confidence intervals for the results. However, such error propagation assessments are highly

computationally demanding and time consuming, and to date are rarely performed in ecological studies.

- Validate the predictions based upon species' data on the habitat use and movement flow with field surveys. The final GI results, i.e. Habitat Functionality and Movement Flow, have a precise ecological meaning. Habitat Functionality indicates the amount of expected flow that comes in a pixel, from all other pixels, and Movement Flow indicates the amount of passages through a pixel. It is therefore possible to validate these metrics by comparing them with adequate field data. GPS tracking provides data that is amenable to validate both Habitat Functionality and Movement Flow metrics (Panzacchi et al. 2016). Camera traps, faecal materials and a variety of other sampling methods might also be appropriate.

7 Using GI modelling to support landscape planning: scenarios, cumulative impacts and zonation

One of the goals that the Norwegian Environmental Agency intended for this project was to establish guidelines for producing maps of ecological connectivity (i.e., GI) to support decisions regarding ecologically sustainable land planning. **While GI maps are necessary for sustainable land planning, the maps themselves may not be sufficient to meet the diversity of land planners' needs.** Additional steps may be necessary to create delineated zonation maps and assess either cumulative impacts or the expected impact of specific development scenarios.

The GI protocol we present is possibly the most robust and advanced approach to modelling ecological connectivity currently in use. A major strength of the proposed procedure is its strong theoretical foundations in ecology and network theory, which provides a coherent and formal integration of species-specific statistical models of habitat use and permeability. **Understanding the mechanisms influencing GI enables us to predict how changes in factors affecting these mechanisms (e.g. land use changes) will impact species' distributions.** This is a major advantage over simpler GIS-based approaches that lack a mechanistic understanding of the ecological processes underlying loss of functional habitat and therefore have limited predictive abilities.

The proposed approach to GI modelling provides the necessary ecological information that we can use to support a wide range of conservation or land-planning objectives. *Cumulative impact* is a term with a somewhat ambiguous meaning with different contexts. For example, managers might seek a general understanding of the average cumulative impact of roads with associated powerlines, or the impact tourist cottages and trails might have on a species or group of species. Managers might also want to know whether powerlines generally have a greater impact when they exist alone as opposed to when they are associated with roads, or whether powerlines' impacts are greater in forests or in open areas. In other circumstances, managers might need a *specific assessment of the cumulative impact of specific infrastructures at specific location*, e.g. a specific road, along a specific route, with an associated specific powerline. The former example describes a spatially-implicit cumulative impact assessment, whereas the latter example describes a spatially implicit assessment or scenario analyses. Both examples refer to different types of cumulative impacts, and the assessments are done in different ways that each produce different information.

7.1 Generic, spatially implicit cumulative impacts

We can use the proposed approach to GI modelling to assess the **average, cumulative impacts** of anthropogenic and/or natural stressors. For example, we can estimate the average impact of roads and powerlines (and their possible interactions) on the habitat quality and landscape permeability for the focal species. This is done directly by modelling habitat quality and permeability, based upon all available observed interactions between the focal species and the focal infrastructure. Specifically, these types of cumulative impacts are quantified by **Resource Selection Functions** and **Step Selection Functions**, which estimate the average effect of each infrastructure type or stressor (given other stressors) and allow combining their collective effects to assess the habitat quality or friction provided by each pixel. Therefore, step 2 and 3 in our protocol (**Figure 2**) explicitly create a model for the combined (or cumulated) effects of different types of infrastructures (Panzacchi et al. 2013). The outputs are numbers that synthesize, and maps that illustrate, the average impact of the focal infrastructures (e.g. roads, buildings etc) on the habitat quality and on the landscape permeability for the focal species while accounting for the effect of all other landscape elements. Such analyses provide a *general* (not specific for a given built infrastructure at a specific location), *spatially-implicit* (not considering connectivity) assessment of cumulative impacts, which can be useful in the early phases of land planning by providing a preliminary idea of the possible impact of building one type of infrastructure instead of another.

7.2 Specific, spatially explicit cumulative impacts: scenario analyses

More comprehensive assessments of cumulative impacts extend beyond the immediate area surrounding a planned development (the potential stressor) at spatial scale that is relevant for a focal species that may be affected. For instance, if the plan was to build an infrastructure network in the middle of an important corridor for a long-distance migratory species, the resulting loss in landscape permeability might be so devastating that it leads to a population's extinction. Alternatively, the same infrastructure network could be built in an area with marginal importance and therefore have a negligible effect. In most cases, we can expect that development will decrease the functionality of an area and change species' movement corridors. The extent of this impact, however, can vary considerably with both the type of and location of construction, with respect to the species most important habitat. **It is therefore crucial to extend information on habitat loss and fragmentation from the local scale to the scale that is relevant for the species' ecology.** This is precisely the role of the *Habitat Functionality* and *Movement Flow* metrics, as their spatial-network approach allows to integrate (or cumulate) impacts over different locations. By combining both types of cumulative impacts (i.e. local, with several stressors and global, across different spatial scales), the proposed protocol is extremely well-suited for assisting land managers with the comprehensive assessment of cumulative impacts at the landscape scale.

The proposed approach to GI modelling provides the formal integration between habitat quality and permeability that is necessary to further assess the **specific, spatially explicit cumulative impacts** of any planned specific anthropogenic and/or natural stressors in a specific area, using **scenario analysis**. This represents the most innovative and useful tool for land planning because the impact of any development will depend on the spatial configuration of the area and its importance for species, as well as the specific characteristics of the planned land use change/infrastructure. When used in scenario analyses, this approach to GI modelling can support land management by quantifying and visualizing the predicted impact of both past and future (expected, plausible or planned) landscape changes on the focal species. Scenario analyses are a very useful tool for both impact assessment and strategic planning at local, regional and national scales.

The process begins by first aggregating georeferenced (pixel-based) values describing the *Habitat Functionality* of a specific landscape, to reflect the overall functionality of the current landscape for the focal species. Then, we forecast the impact of future landscape changes by building a scenario (e.g., the construction of a new highway) and generate new habitat quality and movement friction maps that correspond to these changes. We then re-model GI and calculate a new value of *Habitat Functionality* reflecting the construction of the planned highway. We can assess the proportional impact of the planned infrastructure on the GI for the focal species or species group by comparing *Habitat Functionality* of the current landscape and the highway-scenario, as well as see the predicted changes in movement flow/corridors.

Not only can this approach be used to forecast expected impacts on species according to future scenarios of land-changes, it can also be helpful to quantify **present cumulative impacts of existing infrastructures**. This can be done by obtaining historical maps of the areas before the infrastructures of interest were constructed (or simply removing the focal infrastructure from the quality and friction maps) and re-calculating *Habitat Functionality* and *Movement Flow* for the **past scenario**. Comparing the landscape's *Habitat Functionality* from before and after the infrastructure was built will provide an indication of the infrastructure's impact on functional habitat. Furthermore, *Movement Flow* outputs could illustrate which changes in movement flow can be attributed to past landscape changes.

Authors of this report are involved in several ongoing and new research projects that use *Habitat Functionality* and *Movement Flow* in scenario analyses at the regional, national and Scandinavian scale. For instance, the ongoing **Norwegian Research Council project**

RenewableReindeer (led by authors of this report) explores how climatic changes, existing infrastructure network, planned changes in the infrastructure (hydropower, transportation, tourism), and possible changes in the intensity of use of tourist areas impact wild reindeer populations. As a part of this work, researchers are also assessing the potential impact of alternative mitigation measures to guide sustainable land planning in Norway.

7.3 Identify areas for protection and restoration priority

The proposed approach to GI modelling also provides the formal integration between habitat quality and permeability necessary to further develop synthetic tools for identifying **areas for conservation protection or restoration**. Such analyses can help develop conservation plans or sustainable development plans by identify the most crucial GI areas to be protected, and areas where infrastructure development is expected to cause the smallest impacts on species' functional connectivity. This also represents the most innovative, challenging and possibly among the most useful tools for conservation and sustainable land planning before specific land plans are being developed. This is a field of research under rapid and active development (and a focus of the ongoing **Norwegian Research Council project One-Impact**, led by authors of this report).

The GI models we present here provide possibly the best approach available for depicting the individual pixels' contributions to connectivity for a focal species or dispersal guild, but pixelated surfaces do not automatically correspond with delineated areas for which planners can designate an intended use. Procedurally, it would be straightforward to convert a raster surface to a vector (shapefile) by grouping pixels with *Habitat Functionality* or *Movement Flow* values above a certain threshold and converting them to areas belonging to categories along a gradient of importance (i.e., very important, important, moderately important, unimportant, etc.). However, doing this would completely misinterpret the information contained in the model outputs and we strongly advise against doing so. The GI model is designed to capture the complex interactions between species and habitat in an ecologically relevant manner. Accordingly, it represents the interactions between the habitat quality and the accessibility of each pixel in the landscape, based upon the species-specific movement patterns. **Each pixel in the resulting GI models is intrinsically part of an intricated network representing habitat quality and habitat connectivity calculated over all pixels in the network. Using threshold values to group pixels would therefore defeat the original purpose of the GI analyses.**

Sensitivity analyses represent a more theoretically grounded approach to identify areas for either conservation or restoration. Sensitivity analyses of *Habitat Functionality* or *Movement Flow* metrics can identify which pixels, or groups of pixels, are most important for maintaining the connectivity of high-quality areas (the "integrity of the spatial graph", in graph-theoretical terminology). The analysis involves *removing* one pixel or group of pixels at a time and recalculating the loss in *habitat functionality*. This could start with one species, and potentially scales up to include other species. By repeating the procedure throughout the landscape, we can identify **pixels whose removal would cause the largest impact on functionality or connectivity, and therefore should be prioritized for conservation.**

A similar analysis that iteratively *adds* pixels one at a time and calculates the corresponding effect on quality or connectivity of each pixel in the landscape, will **identify pixels whose restoration would lead to the greatest increase in habitat functionality and which should be prioritized for restoration.** For example, if we want to determine the best place to position a wildlife passage along a roadway, we can iteratively transform one "road pixel" (i.e. poor-quality habitat) into a "high-quality pixel" for each pixel comprising the road to simulate the construction of a wildlife bridge. This will identify where a new wildlife overpass would lead to the largest increase in *Habitat Functionality* (or *Movement Flow*) for the species. McRea et al. (2012) provide an example of applying this approach on simulated landscapes.

Areas identified through sensitivity analyses are also particularly well suited for addressing the land management issues that involve enforcing no-net-loss regulations. Through scenario analyses, we can assess if we can expect areas containing new habitat created to compensate for habitat replaced by infrastructure to provide the equivalent *functional habitat* of what was lost. The functionality of new habitat will depend heavily on its spatial relationship to other GI, which is best assessed through a mechanistically-based model.

The basic principle of the sensitivity analysis (i.e. the iterative removal of one pixel at the time followed by a re-assessment of the corresponding loss in habitat functionality) is the core of most popular software options in use for identifying areas to be prioritized for conservation or restoration. **Zonation** (Moilanen et al. 2014) is software that uses a deterministic approach to produce a hierarchical prioritization of the landscape by iteratively removing the least valuable remaining cell while accounting for connectivity and generalized complementarity. The removal procedure therefore stops when the remaining area fits with the remaining conservation budget available to land planners. However, Zonation is primarily a *Multi-Criteria-Decision tool*, designed to identify areas that can be protected within the constraints presented by the economic cost of conservation while also accounting for other factors such as land ownership, administrative boundaries, etc. Similarly, **Marxan** (Ball et al. 2009; <http://marxan.net/>) is another *Multi-Criteria-Decision tool*, designed for meeting specified ecological targets, while minimizing the costs of protection. Both software packages operate within an optimization framework that attempts to identify the most cost-efficient trade-off among a set of options. A review of the relevance and robustness of multicriteria decision tools is beyond the scope of this pilot project. See Delavenne et al. (2011) for a comparison of Zonation and Marxan software.

7.4 Optimizing GI models for efficient implementation

Within network theory, the metrics we produce can be described as “*all-pixels centrality metrics*”. This implies that the final value attributed to each pixel representing GI synthesizes the properties of all pixels in the entire graph (i.e. landscape), in terms of both habitat quality and movement-based connectivity. In sensitivity analyses, these calculations must be repeated thousands of times, possibly for each pixel in the landscape. This can be computationally challenging in very large, high-resolution landscapes. The algorithms we use presently have been developed in collaboration with computer scientists and mathematicians and optimized to run over relatively large landscapes. For this study, each GI infrastructure model run from several minutes to a couple of hours on a standard laptop, on an area of 15 x 27 km, 100 x 100 m pixels. This is a very good performance, compared to that of other similar software packages available. However, we have tested alternative approaches that can speed up calculations substantially for use in very large landscapes. Our research team is currently pursuing cutting-edge mathematical and computational solutions to allow for faster computations of movement-based habitat connectivity and Green Infrastructures over large, continuous, high resolution landscapes.

7.5 Options for implementing standardized connectivity analyses for use in municipal planning

The goal of this project, as stated by the NEA in its call for proposals, is to “*eventually develop a product or service (for analysing Green Infrastructure) that can be used in all municipalities over the entire country.*” In this chapter, we present preliminary reflections on how the NEA might eventually achieve this goal. We envision, in general terms, how responsibilities for various tasks would be distributed—as well as what each option would require in terms of expertise, computing capacity and system maintenance for the entities involved. We also provide our reflections on the expected costs, and the expected utility of the outputs that each option might generate.

7.5.1 Interactive green infrastructure map

One strategy would be for the NEA to contract a separate entity (i.e., a research institute or an academic institution) to perform the connectivity analyses and generate maps of green infrastructure that cover all municipalities. Maps would be distributed to municipal planners and decision makers through an interactive web-based platform, and updated at regular intervals (i.e., 3-5 years) using resolutions that are suitable for municipal planning processes. The group responsible for conducting the analyses would have the expertise and familiarity with scientific progress in connectivity research and therefore be capable of using the most current connectivity algorithms. Municipal employees would thus have access to GI maps, and possibly other products useful for land planning, to be agreed upon.

This option represents a very simple solution for the municipalities' planners and decision makers, because all responsibility for conducting analyses and generating maps rests with the group contracted by the NEA. It also represents a comparatively easy solution for the entity responsible for the maps because they are in control of the entire analytical and mapping process, and because they can follow a standardized protocol for all municipalities. This option also provides a higher potential for quality assurance regarding using the most current and relevant algorithms and data than if analyses and map generation were decentralized. A centralized approach also insures that connectivity maps generated for municipalities in Norway will be coherent across scales and capable of being used in regional planning processes. We also see this option as the least expensive of the alternatives we present, since it does not involve extensive software development, personnel training, or significant amounts of user support.

This approach does, however, have some substantial disadvantages. The most significant is the inflexibility it presents to municipalities. The connectivity maps are essentially static and user interaction is limited to zooming in or out. Using this approach, only the entity that generated the maps would be capable of accessing the algorithms and using scenario analyses to explore the potential consequences of proposed development strategies.

7.5.2 Plugins for GIS and/or stand-alone programs

A second option would involve generating plugins for GIS software, or potentially a stand-alone software package (**Figure 21**). The NEA would contract an entity (i.e., research institute, academic institution, or software developer) to generate the software and support—including user guidelines, required updates and debugging work. This solution would be similar to existing software packages available for connectivity analyses, such as Circuitscape (McRae et al. 2016) and GFlow (Quinby et al. 1999), although ideally tailored to meet land planners needs for Norway's biota. Land planning personnel from each municipality could install the software, and its periodic updates. Using the software would require municipality personnel to receive training so that they are familiar with software guidelines. Municipal personnel would also bear the responsibility of downloading relevant data for performing the analyses when they are needed and generating the maps from analyses' outputs.

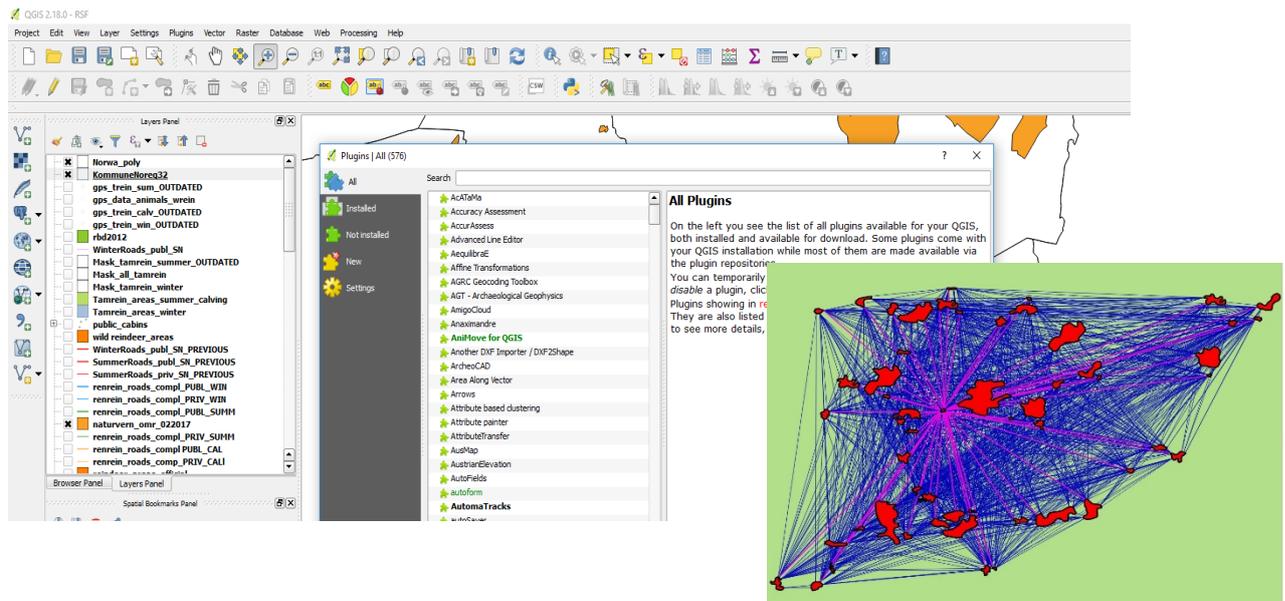


Figure 21. Screenshot of a connectivity plugin within a QGIS platform, together with an illustration of a potential connectivity analysis output map.

This approach represents a comparatively simple option for the entity responsible for generating the software. Once the software is produced, it becomes the responsibility of municipalities' personnel to conduct the analyses and generate whatever maps they feel they need. This approach gives municipalities a high degree of freedom to select the most appropriate data and tailor the analyses to best inform their proposed land management strategies. This access to the analytical process also enables producing scenario analyses and prioritization of conservation measures or comparing the impacts of several alternative land management or development strategies.

We see several important disadvantages to this approach, however. This option would be demanding for the municipalities, because it will require that municipality personnel obtain technical familiarity with the analytical software. We can expect that the analytical expertise of land planning personnel may vary among municipalities, which may lead to variation in the quality of the analytical work and the correct application of the software. Municipalities will need to have enough computational capacity to use the software, a requirement that might exceed the computing power of their current hardware. Importantly, implementation of this decentralized analytical approach would require a research institute to synthesise all relevant information regarding habitat preferences and movement capabilities for a wide range of species and establish a database infrastructure that would provide municipalities with easy access to these data, together with a wide range of environmental data they would need for connectivity analyses. The NEA would need to ensure that these databases are regularly updated to minimize the time gap between when new data are collected and when they become available at a national scale.

We also foresee a challenge in ensuring the quality of the results, as they are produced independently by each Municipality. This option also presents challenges with integrating results from analyses from several separate municipalities at larger spatial scales for regional or national connectivity plans. Contiguous municipalities may use different data and procedures, and thus reach different conclusions regarding areas of common interest for large scale connectivity. Finally, we see a considerable economic cost to this approach as well. Implementing analytical algorithms into a plug in or software may be straightforward. However, making the software user friendly to a user group without a research background will involve far more effort and expense.

7.5.3 Web-based software and services

A third option entails establishing a web-based tool, where a research institute, academic institution or consulting firm is assigned responsibility to develop and host analytical software for analysis and map generation. With a web-based interface, municipality land planning personnel can help define the conditions for the analyses and which scenarios they wish to explore and can do so when the results of these analyses are needed. The web-based tool would also be linked to most current versions of the appropriate datasets necessary for whichever analytical procedure the municipality might request and operate on a server that has enough computational power to perform the analyses. This option would be as technically straightforward for municipality personnel as the first option described above, because they are not expected to possess any analytical expertise related to the algorithms the software uses, nor would the municipalities need to have computational power to run the algorithms. This simplicity would thereby lower the expected economic impact for each municipality.

Centralizing the analytical processes in an adaptable web-based tool would entail greater level of quality control, with results that are appropriate for use at several spatial scales. There is also an improved level of scientific integrity compared with software used individually by each municipality. Developers of the web-based tool can more easily integrate updates in connectivity algorithms resulting from the most current advancements in connectivity research, without needing to redesign software, issuing updated versions, or providing regular training of municipality personnel regarding its use.

This option provides municipalities the greatest flexibility to use connectivity analyses exploring conservation and restoration scenarios and prioritizing areas, at a substantially lower economic cost to the individual municipalities. This does not imply that the option is itself inexpensive. Developing a web-based tool will likely involve a considerable expense for the NEA, and likely more than developing a stand-alone software package or GIS plugin we present as the second option. There will also be additional expense associated with maintaining the server necessary for this tool. Finally, the tool will require monitoring and maintenance to guarantee that it performs properly. Online tools are relatively young technologies, and it is difficult to anticipate all the eventualities.

Despite the potential for requiring a greater economic investment in developing and maintaining an online tool, it seems likely that this third option represents the best approach. Its flexibility and scalability would provide the greatest utility for implementing connectivity analyses at multiple administrative scales, with the highest quality control, with a total economic cost that would be less than if municipalities were asked to conduct their own connectivity analyses using software developed for the NEA.

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