

1 Estimating the cumulative impacts and the zone of influence  
2 from multiple anthropogenic infrastructure on biodiversity

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## Abstract

1. Most infrastructure and land use change from industrial development take place in landscapes already affected by multiple human disturbances, leading to cumulative impacts on biodiversity. Typically, the effect of infrastructure is determined by computing the distance to the nearest feature only, ignoring their potential to sum up. Here we propose an approach to estimate the magnitude and the zone of influence (ZoI) of the impacts of multiple features of a given type of infrastructure and test if they accumulate.
2. First, we derive the estimation methods based on the influence from the nearest feature only and the cumulative influence of multiple features. Second, we perform simulations to investigate under which conditions these two measures of influence represent different gradients of spatial variation. We show the two measures are more correlated either when the spatial distribution of features is sparse and the ZoI is small or when features are clustered and ZoI is large.
3. Finally, we illustrate this approach by assessing the cumulative impacts of tourism facilities on the space use of mountain reindeer, a species highly sensible to anthropogenic activity and infrastructure. We present strong evidence of cumulative impacts of private cottages and tourist cabins on reindeer habitat selection, with zones of influence of 10 and 20 km, respectively. This means that considering only the influence of the nearest feature, as it is common in applied studies, disregards the possibility of cumulative impacts and might limit our understanding of the impacts of landscape change on biodiversity.
4. *Synthesis and applications.* We developed an approach to assess cumulative impacts of infrastructure on biodiversity and ecosystems, with direct application in environmental and strategic impact assessment and integrated land use planning. The two influence measures are calculated before statistical analysis, making them computationally efficient and flexible in terms of the choice of influence shape within the ZoI. Both of them can be easily computed in R and GRASS GIS through the `oneimpact` R package. Even though our examples focus on animal space use, the approach can be easily extended to ecological studies and impact assessments over several fields, from genetics to organisms to populations and communities.

46 **Key-words:** (choose up to 8) cumulative effects, piece-meal development, Anthropocene, habitat frag-  
47 mentation, habitat loss, *Rangifer tarandus*, density, nearest neighbor distance, scale of effect, kernel filter,  
48 distance-weighting

# 1 Introduction

Human-induced land cover modifications and infrastructure from industrial development are widespread and increasing at an accelerated pace across all regions of the world (Venter *et al.*, 2016; Ibisch *et al.*, 2016), including all global biodiversity hotspots (Sloan *et al.*, 2014), and are among the main causes of biodiversity declines (Benítez-López *et al.*, 2010; Newbold *et al.*, 2015). Most new landscape changes take place not in intact habitats but in landscapes already affected by multiple disturbances to wildlife (Barber *et al.*, 2014). As a consequence, the effects of such new modifications might accumulate and interact in complex ways with the preexisting anthropogenic stressors, leading to cumulative impacts (Box 1; Gillingham *et al.*, 2016) – synergistic, interactive, or unpredictable outcomes, different from those of each separate source of disturbance (Johnson & St-Laurent, 2011). Indeed, cumulative impacts are a central issue in ecological studies and environmental impact assessments and a priority for making effective, knowledge-based decisions on land use planning, designing mitigation actions, and avoiding higher impacts of industrial development on ecosystems (Gillingham *et al.*, 2016; Laurance & Arrea, 2017). Most environmental impact assessment studies still focus on single projects at small spatiotemporal scales (Johnson, 2011), and even ecological studies conducted at larger extents generally consider only the effect the nearest feature of each infrastructure type (e.g. Torres *et al.*, 2016). Here we propose an approach to assess the impacts of multiple features of a given type of infrastructure on biodiversity and test if they accumulate.

Anthropogenic infrastructure have direct consequences in the area where they are built (e.g. habitat modification or road kills), but might also indirectly affect species and ecological processes up to several kilometers from the infrastructure locations (e.g. reducing the probability of animal occurrence Johnson *et al.*, 2005; Torres *et al.*, 2016). Therefore, two intrinsically related dimensions of impacts to be assessed in impact studies are the magnitude of the impact and the size of the affected area (Box 1; Johnson & St-Laurent, 2011). The *effect size* or *magnitude of the impact* represents how strongly different factors influence focal organisms and processes and is generally estimated through a combination of biological and environmental data and statistical modeling (Box 1; Polfus *et al.*, 2011). The spatiotemporal *zone of influence* (ZoI) corresponds to the area (and sometimes the period) within which there are detectable impacts from different landscape modifications on the process of interest, but is commonly expressed in terms of distances — the distance from or radius around the disturbance sources which defines the affected area (Box 1; Boulanger *et al.*, 2012).

Infrastructure and disturbance impacts can accumulate over time and space, as a result of the sum or interaction of the impacts of different types of infrastructure or multiple features of same-type infrastructure.

80 The cumulative influence of multiple infrastructure of the same type – our focus here – is most commonly  
81 either appraised by changing the variable’s level of spatial organization (e.g. urban areas or wind parks  
82 instead of a combination of buildings and turbines, respectively) or ignored by considering only the effect  
83 of the nearest infrastructure feature (e.g. Torres *et al.*, 2016). When determining the ZoI, the concept of  
84 ecological threshold and analytical procedures developed therein are commonly used (Ficetola & Denoël,  
85 2009). Under this framework, the estimation of the ZoI is often carried out by fitting piece-wise regression  
86 or other non-linear regression models (such as an exponential decay or generalized additive models; Skarin  
87 *et al.*, 2018; Ficetola & Denoël, 2009) to the measured response of an ecosystem as a function of distance  
88 to an infrastructure. This distance is typically the distance to the nearest instance of this infrastructure type,  
89 ignoring potential cumulative effects of multiple instances of an infrastructure. Besides, this approach  
90 is generally limited to the assessment of thresholds for only one or a few types of infrastructure (e.g.  
91 Boulanger *et al.*, 2012), since its computation requires repeated fitting and might become impracticable for  
92 a large number of factors (Lee *et al.*, 2020).

93 Another approach to estimate the ZoI may be found under the umbrella of the discussion about spatial  
94 and temporal *scales of effect* in the evaluation of species-landscape relationships. In this context, the  
95 number of features is averaged for multiple spatial extents surrounding focal study sites (Jackson & Fahrig,  
96 2015) or considering different grains (Laforge *et al.*, 2015), or weighted using neighborhood analysis over  
97 several different extents or radii (generally termed “scales”), creating a series of infrastructure density  
98 maps (McGarigal *et al.*, 2016). These spatial extents and grains are generally linked to the spatial and  
99 temporal dimensions of the infrastructure considered, as well as to the expected temporal scale of the  
100 biological response to such infrastructure. Each of these maps is tested against the ecological response  
101 variables to assess the extent at which the impact is stronger, most commonly through measures of model  
102 performance and explanatory power such as  $R^2$ , AIC, or BIC, or evaluating the variation in fitted model  
103 coefficients (Jackson & Fahrig, 2015; Huais, 2018) – what is called a multi-scale approach (e.g. Zeller  
104 *et al.*, 2017). Multi-scale analyses brought important advances for landscape and environmental impact  
105 studies (e.g. McGarigal *et al.*, 2016), even though in many of them the scale of effect was not properly  
106 evaluated (Jackson & Fahrig, 2015). However, the key here is that these approaches have hardly been put  
107 into the framework of cumulative impact assessment (but see Polfus *et al.*, 2011).

108 We propose an approach to estimate the magnitude and the ZoI of the impacts of multiple features of an  
109 infrastructure and test if they accumulate. First, we derive the estimation methods based on either the in-  
110 fluence from the nearest feature only or the cumulative influence of multiple features (Box 1, Fig. 1), using

111 habitat selection analyses as example. Second, we perform simulations to distinguish in which conditions  
112 these two measures of influence represent similar or different spatial gradients, to aid the interpretation of  
113 estimated impacts based on each of them. Finally, we illustrate our approach by assessing the cumulative  
114 effects on the space use of the tundra's flagship species, the mountain reindeer (*Rangifer tarandus taran-*  
115 *dus*). We also provide tools to allow an easy implementation of the cumulative approach presented here in  
116 R (R Core Team, 2020) and GRASS GIS (GRASS Development Team, 2017) through the `oneimpact` R  
117 package.

## Box 1 – Definitions

**Impact** The term is used here to represent the consequences of human-made and industrial landscape changes on a focal ecological response variable, such as measures of biodiversity or ecological processes. Thus, impacts represent the functional responses of species and processes to human activity (Johnson & St-Laurent, 2011). We analytically decompose the impacts into their **magnitude** and **zone of influence (ZoI)**. A given infrastructure (e.g. tourist cabin) might affect a certain process (e.g. an species occurrence) strongly or weakly (magnitude), and this impact might decrease fast with distance or extend over several kilometers (ZoI).

**Cumulative impacts** can result from the interaction between multiple features of an infrastructure – our focus here – but also from the effects of different types infrastructure (e.g. houses, turbines, roads, dams) or from top-down or bottom-up ecological cascades. Cumulative impacts of multiple features depend on the number of features in an area, their spatial distribution, and co-occurrence with other infrastructure types, and might differ for distinct species, values, or processes – possibly leading to stronger negative impacts for some or even to benefits for others, if compared to the impact of a single infrastructure.

**Magnitude of the impact** It describes how strong is the effect of a variable over a given biological response, and is described here by the model coefficients ( $\beta$ 's in eq. 1).

**Influence** The term is used here in a pragmatic way and represents the function  $\phi$  that sets how the impacts of an infrastructure feature change with the distance to such feature, and is the basis for defining the ZoI. The influence of a feature might follow different **influence functions** (also called weighting functions, smoothing filters, or decay functions). It can be constant up to a given threshold distance or decrease in different ways with increasing distance from it (Fig. 1A). When multiple features of an infrastructure are present, one can assume that either only the nearest feature affect the response (eq. 3) or that the influence of multiple features accumulate (eq. 4, Fig. 1B).

**Zone of Influence** The **ZoI** is the maximum distance from an infrastructure feature where it influences or affects a given biological response. For non-vanishing functions (e.g. exponential, Gaussian), a threshold must be set to define the ZoI – e.g. the distance at which the influence function goes below 0.05 or 0.01. In the landscape ecology literature the ZoI is often called the *scale of effect* of a given covariate in space (e.g. Jackson & Fahrig, 2015); we use the term ZoI to avoid misunderstandings derived from the different definitions of *scale*.

118

## 2 Deriving the estimation of the cumulative influence of multiple features

120

121 We first derive the cumulative influence of multiple features of an infrastructure type, e.g. roads, houses  
122 or tourist resorts, on space use. To illustrate it, we use as example a habitat selection analysis, which  
123 aim at discriminating what sets of environmental conditions are selected or avoided by animals, based on

ecological data such as species occurrence or movement data and use-availability designs (Fieberg *et al.*, 2021). The main element in habitat selection approaches is the habitat selection function (HSF)  $w(\mathbf{X})$ , a function proportional to the probability of selection of a given space resource unit, depending on the frequency of used and available resource units (Thurfjell *et al.*, 2014). The HSF  $w(\mathbf{X})$  is function of a vector of predictor variables  $\mathbf{X} = X_1, X_2, \dots, X_k$ , which here correspond to  $k$  different types of infrastructure, but might also represent other landscape modifications or spatiotemporal variables. In its parametric form, the HSF might be represented by

$$w(\mathbf{X}) = \exp \left( \beta_0 + \underbrace{\beta_1 X_1}_{\text{A) Infrastructure type 1}} + \underbrace{\beta_2 X_2}_{\text{B) Infrastructure type 2}} + \underbrace{\beta_{12} X_1 X_2}_{\text{D) Interaction infrastructure types 1 and 2}} + \dots + \underbrace{\beta_k X_k}_{\text{C) Infrastructure type k}} \right) \quad (1)$$

where  $\beta_k$  represents the magnitude of the impact (coefficient or effect size) of the infrastructure of type  $k$ . In its simplest form, here *the cumulative impact of different types of infrastructure* is given by the additive effects of the  $k$  infrastructure types (e.g. terms A, B, and C in equation 1) and possibly by interaction terms between variables (such as term D in equation 1, with an interaction coefficient  $\beta_{12}$ ), that allow for non-linear, joint effects caused by the co-occurrence of different types of infrastructure.

To derive the cumulative impact of multiple infrastructure of the same type, we start by defining verbally two representations of the spatial influence of infrastructure: the influence of the nearest feature alone and the cumulative influence of multiple features (Box 1, Fig. 1). Note that we refer to the term “influence” instead of “distance”, since we are generally referring to decay functions that decrease towards zero as the Euclidean distance from the infrastructure increases, and possibly vanish at a given point (the zone of influence).

First, within the ZoI, the influence of an infrastructure feature (e.g. a house or road) might follow different functions – it can be either constant (threshold curve, Fig. 1A) or decrease as one moves away from the infrastructure (e.g. linear and Gaussian curves, Fig. 1A). Whether the influence of a given infrastructure follows one of these or other functions is to be determined empirically (Miguet *et al.*, 2017). The simplest assumption, widely used in the literature, is that all the area within the ZoI is affected equally (e.g. Quiñonez-Piñón *et al.*, 2007), even though it might be more reasonable to consider that the influence is higher close to the infrastructure (Skarin *et al.*, 2018; Zeller *et al.*, 2017). Second, the effect of the infrastructure might depend either on the nearest infrastructure alone or on the cumulative influence of several



150 infrastructure (Fig. 1B). In the former case, the influence is similar when one approaches a single, isolated  
 151 house or a small village, for example. In the latter, the influence of nearby houses accumulate and might  
 152 be greater than that of a single, isolated house.

153 [Figure 1 about here.]

154 To translate those representations into a mathematical form, now we decompose each of the linear terms  
 155 (i.e. A, B, C, ...), in equation 1. Suppose that in the landscape there are  $n_k$  features of the same type of  
 156 infrastructure  $k$ , and let the influence of the feature  $i$  of an infrastructure  $k$  follow an influence function  
 157 (or “weighting function”, Miguet *et al.*, 2017)  $\phi_{i_k} = f(d_{i_k}; ZoI_k)$ , where  $d_{i_k}$  is the distance to a feature  
 158 ( $i_k$ ) of infrastructure type  $k$  and  $ZoI_k$  is its zone of influence. Figure 1A shows a few possible shapes for  
 159 the function  $\phi_{i_k}$ . We can sum the effect of each feature on animal space use, so that the linear terms in  
 160 equation 1 becomes:

$$\beta_k X_k = \sum_{i=1}^{n_k} \beta_{i_k} \phi_{i_k} \quad (2)$$

161 Typically, only the nearest feature is considered, resulting on the implicit assumption that  $\beta_i = 0$  for all  
 162  $i > 1$  (where the features are ordered by increasing distance). Thus, eq. 2 turns into:

$$\begin{aligned} \beta_k X_k &= \beta_{1_k} \phi_{1_k} \\ &= \beta_{1_k} \phi_{nearest_k} \end{aligned} \quad (3)$$

163 where  $\phi_{nearest_k}$  is the influence of the nearest feature ( $i = 1$ ) of the infrastructure type  $k$  (see Fig. 1B).  
 164 However, possibly a more reasonable assumption would be that  $\beta_{i_k} = \beta_{(i+1)_k} = \beta_{(i+2)_k} = \dots = \beta_k$ , i.e.  
 165 that all features of a given type present the same influence around them and all  $\beta$ 's are identical. Thus, eq.  
 166 2 is reduced to:

$$\begin{aligned} \beta_k X_k &= \beta_k \sum_{i=1}^{n_k} \phi_{i_k} \\ &= \beta_k \phi_{cum_k} \end{aligned} \quad (4)$$

167 where  $\phi_{cum_k} = \sum_{i=1}^{n_k} \phi_{i_k}$  is the cumulative influence measure and is proportional to the “density” of  
 168 features in space (e.g. Panzacchi *et al.*, 2015). The cumulative influence measure is easily calculated using  
 169 geographical information systems, e.g. through neighborhood analysis, and can be rescaled to meaningful  
 170 measurement scales, such as the number of point features per km<sup>2</sup>. For the derivation of similar equations  
 171 for variables represented as lines and areas, see Appendix A.

### 172 **3 When do the influence of the nearest feature and the cumulative** 173 **influence represent similar spatial variation?**

174 A deeper look at the two influence measures – nearest and cumulative – is important to interpret them  
 175 in ecological contexts and to investigate in which conditions they represent similar or different gradients  
 176 of spatial variation. Their similarity depends on the spatial distribution of the infrastructure as well as  
 177 its zone of influence, and might affect our ability to distinguish among their effects in real landscapes.  
 178 To illustrate in which conditions they converge, we simulated  $30 \times 30$  km<sup>2</sup> landscapes with a constant  
 179 number of point features (e.g. houses, cabins, turbines;  $n = 100$ ) distributed following different spatial  
 180 patterns, in a gradient of clustering, from regular and random to clustered (Fig. 2; Appendix B). For each  
 181 landscape we calculated the two measures of influence ( $\phi_{nearest}$  and  $\phi_{cum}$ ) for a range of values of ZoI  
 182 (from 0.06% to 40% of the landscape extent), using a linear decay function (Fig. 1). We then compared  
 183 the resulting influence spatial patterns through Pearson correlation of the values of the two measures at the  
 184 same coordinates.

185 [Figure 2 about here.]

186 When  $ZoI/2$  is smaller than the minimum distance between features, both measures of influence are  
 187 identical (Fig. 2; correlation = 1 for all ZoI values below the black dashed vertical line). This happens  
 188 because the ZoI of each feature is not large enough to interact with each other. This happens when either  
 189 the ZoI is small enough or there is a small number of features sparsely distributed in space. As the ZoI  
 190 increases, the effect of nearby features starts to accumulate and the two measures of influence begin to  
 191 represent different patterns of spatial variation. This is valid for scenarios with random, regular, and slightly  
 192 clustered distributions of infrastructure features (Fig. 2A,B, Fig BXX). In contrast, as the distribution of  
 193 features gets more clumped and distributed in smaller clusters (up to a limit with a single small cluster, Fig.  
 194 2C), the correlation between the influence measures goes through a point of inflection as the ZoI increases,  
 195 beyond which it increases with ZoI (Fig. BYY). The point where the correlation between the influence

measures stop decreasing is defined by the size of the clusters (grey dashed vertical line in Figs. 2B,C). For ZoI values larger than the cluster size, the two influence measures start to converge again. This happens because, while the variation in cumulative influence increases continuously with ZoI, the variation in the influence of the nearest feature tends to get stable for large enough ZoI values (Fig. BZZ). That is the point beyond which it might get harder to distinguish between the effect of each feature alone, regardless of the influence measure, and the effect of a collection of features transforms into that of a “super-feature” (e.g. groups of houses or wind turbines behave as urban areas or wind parks, respectively). When the correlation between influence measures is higher, it might be difficult to distinguish whether the impacts of a given infrastructure type accumulate or not. However, whether a given biological response variable is affected by only the nearest feature or the cumulative influence of multiple features (or none) remain an empirical question to be explored in real landscapes.

## **4 Empirical demonstration: cumulative influence of infrastructure on reindeer space use**

### **4.1 Study area, ecological data, and methods**

In our empirical demonstration we aimed to assess if and how the impacts of multiple infrastructure affect mountain reindeer space use during summer in Southern Norway. Reindeer are highly sensible to human activity, and the wild populations in Norway are the last remaining ones of this species in Europe. We used GPS tracking data from the Hardangervidda reindeer population, the largest population of wild mountain reindeer (Fig. 4). During summer, the area is mostly used for tourism. It has 14,154 private cottages, 26 large tourist cabins, and hundreds of kilometers of trails, besides roads and small tourist cabins (Fig. C2). We used data from 48 (??) female reindeer collected between 2001 and 2010 (see Panzacchi *et al.*, 2015, for further details) and selected July as a month representative of the summer. To assess reindeer habitat selection using a use-availability setup, each used GPS point was compared against 9 available locations created at random within the area occupied by the population (Fig. 4) and annotated with environmental covariates.

To account for bio-climatic-geographical variation in environmental characteristics we used the four first components from a large principal component (PC) analysis conducted for Norway (Bakkestuen *et al.*, 2008), which correspond to gradients of (1) PC1 - continentality, (2) PC2 - altitude, (3) PC3 - terrain ruggedness, and (4) PC4 - solar radiation. We included a quadratic term for PC1 and PC2 to account for

niche “optima” (*sensu* Panzacchi *et al.*, 2015). We also used a satellite-based land cover map with 25 vegetation classes, which we further grouped (see Table C2). Because of correlations among covariates, and to keep model fitting relatively simple, we estimated the cumulative impacts for two anthropogenic variables: private cottages and large tourist cabins.

For each infrastructure type we calculated the influence measures for 8 different ZoI, from 100 to 20,000 m. For each ZoI, we used four influence functions, to account for different shapes of the variation of the infrastructure influence within the ZoI (Fig. 1A): threshold, linear decay, Gaussian decay, and exponential decay, and made two assumptions for the impact of additional features, leading to the measures of influence from the nearest feature ( $\phi_{nearest}$ , eq. 3) and cumulative influence ( $\phi_{cum}$ , eq. 4; see Fig. 1B). We then fitted HSFs (eq. 1) combining the effects of infrastructure, land cover, and bio-climatic data through binomial generalized linear models (Fieberg *et al.*, 2021).

Model fitting consisted in two steps. We first fitted single-infrastructure models in a procedure of variable selection (Burnham *et al.*, 2002) to assess the most likely influence functions and ZoI for each infrastructure type, while checking for the correlation between covariates. Single-infrastructure HSF were fitted using the `multifit` function in R (Huais, 2018) and compared using AIC. Second, using the most likely influence functions and ZoI from the single-infrastructure models, we fitted multi-infrastructure HSF to assess the combined impacts of multiple types of infrastructure, in an approach similar to Laforge *et al.* (2015).

To quantify the impacts of infrastructure, we used eq. 2 and multiplied the magnitude of the impacts – the coefficients of the fitted model – by the influence measures included the model. We then estimated habitat suitability by predicting the HSF (eq. 1) over the space and rescaling the predicted values to the interval [0, 1]. For more details on the data, environmental covariates, modeling, and results, see the Appendix C.

## 4.2 Cumulative impacts on reindeer space use

We found strong evidence that the impacts of private cottages and tourist cabins accumulate over reindeer habitat selection, leading them to avoid being close to these infrastructures (Table C2). While private cottages exerted a constant cumulative influence within a ZoI of 10 km, large tourist cabins followed an exponentially decaying cumulative influence in a ZoI of 20 km (Fig. 3; Table C2). Notice that, as parameterized here, for the tourist cabins an exponential decay with ZoI of 20 km means that the influence of cabins decrease to half of its maximum value at ca. 5 km from the infrastructure (Fig. 3). As a comparison, the most plausible model with a covariate for the influence of the nearest feature was ranked 26<sup>th</sup> in the model selection ( $\Delta AIC = 921$ ), and the most likely model including the log-distance to the

255 nearest feature was ranked 44<sup>th</sup> ( $\Delta AIC = 1197$ , Table C2).

256 [Figure 3 about here.]

257 The estimated magnitude of the impact of a single private cottage ( $\beta_{cottage} = -0.0081$ ) was much smaller  
258 than that of a single tourist cabin ( $\beta_{private\ cabin} = -2.654$ ; Fig. 3A, Table C3), which is reasonable since  
259 the former are used by much less people than the latter. However, since private cottages occur at higher  
260 densities, in some areas their overall impact is larger than that of tourist cabins. If we take the areas with  
261 the higher cumulative influence of infrastructure in Hardangervidda – where the number of private cottages  
262 sum to 2664 and the (exponentially weighted) number of tourist cabins sum to 5 – the impact of private  
263 cottages agglomerates is nearly twice that of tourist cabins (Fig. 3B and 4). Following the HSF coefficient  
264 interpretation from Fieberg *et al.* (2021), considering that all other conditions are kept similar, a reindeer  
265 avoids an area 14.43 times more strongly than another area with 330 less private cottages in a radius of 10  
266 km. That is approximately the same difference in avoidance a reindeer presents among two areas that differ  
267 in 1 tourist cabin in a radius of 20 km (Appendix C).

268 When cumulative impacts of infrastructure are predicted in space by multiplying the magnitude of the  
269 impacts to the cumulative influence measures (eq. 4), we see how the relative impact of private cottages  
270 and tourist cabins changes across space (Fig. 4). While the impact value for private cottage rises to ca. 20  
271 in the areas with the highest cumulative influence of cottages, it hardly goes above 10 for tourist cabins.  
272 As a consequence of the combined impact of multiple infrastructure, and given reindeer avoided high  
273 densities of both infrastructure types at relatively large extents, areas of high habitat suitability for reindeer  
274 correspond to those in which the cumulative influence of both infrastructure is low – what matches the  
275 locations used by reindeer, indicated through the GPS data (Fig. 4).

276 [Figure 4 about here.]

## 277 5 Discussion

278 There is an urge to evaluate, debate, and inform scientists, decision-makers, and the public in general about  
279 the past, current, and future effects of global infrastructure on biodiversity (Laurance, 2018). Most of the  
280 decisions and regulations made for infrastructure projects are performed with little knowledge about the  
281 multiple potential impacts on the ecosystems where they are built and the species living therein. Even  
282 when environmental impact assessments are well conducted, they hardly estimate the cumulative effects  
283 of those infrastructure with pre-existing ones or with other development projects planned for the same

region (Laurance & Arrea, 2017; Johnson, 2011). In great part, this happens because current approaches and tools still lack in their ability to incorporate cumulative impacts (but see Gillingham *et al.*, 2016, for recent advances). Building upon previous frameworks to understand cumulative impacts (Johnson & St-Laurent, 2011) and by adapting concepts and tools from the landscape ecology literature into the nearest and cumulative influence measures, here we gave a step further in developing a clear way to assess cumulative effects and impacts of infrastructure on biodiversity. The approach proposed here allows one to: (i) quantify the cumulative impact of multiple infrastructure of the same type, the main focus of our approach; (ii) test whether there are cumulative impacts for each type of infrastructure, by comparing the influence of the nearest feature and the cumulative influence as predictors of biological responses, within ecological models; and (iii) estimate the zone of influence for multiple types of infrastructure.

## 5.1 Applying the cumulative influence approach to impact assessment

In our empirical demonstration with mountain reindeer in Norway, we found a strong support for the hypothesis of cumulative impacts of private cottages and tourist resorts on reindeer habitat selection, with large ZoI – up to 20 km. Quantifying the impacts based on their magnitude and influence function allows us to compare the effects of different types of infrastructure. While the impact of a single cottage is smaller than that of a single tourist cabin, it can be much higher in areas where many private cottages are aggregated, because their influence accumulates over space (Fig. 3 and 4, Fig. C5). We also found all models based on the influence of the nearest feature to be much less supported by the data than the ones incorporating the cumulative influence of multiple features. This includes the models based on the log-distance to the nearest feature, which is a common proxy for the effect of infrastructure and landscape variables in the ecological literature (e.g. Torres *et al.*, 2016; Polfus *et al.*, 2011). This means that, by limiting measures of infrastructure influence to the nearest feature only, researchers and practitioners have been ignoring the possibility of cumulative impacts in ecological studies and impact assessments, what limits our overall understanding of the impacts of landscape change on biodiversity.

Three points must be highlighted regarding the interpretation of the ZoI in real contexts. First, if different influence functions are found to affect the ecological response under study, the ZoI represents distinct areas affected by infrastructure. For instance, while we found a constant influence of private cabins in a ZoI of 10 km, for tourist cabins we found an exponential decay of the influence of these infrastructure as one gets far from them, which means not all 20 km around the resorts are affected equally. Therefore, to understand how the impact of infrastructure change across space it must be assessed by combining the magnitude and the influence function that define the impact (eq. 2, Fig. 3 and 4). Second, as a consequence of different

315 shapes of the influence within the ZoI, the area affected by infrastructure or landscape changes of a given  
 316 type might drastically change. Indeed, in a study on bird and insect abundance, Miguet *et al.* (2017) showed  
 317 that the area affected by landscape variables can increase by a factor of up to 5.7 when one uses a distance-  
 318 weighted influence measure (as the exponential and Gaussian ones presented here), in comparison to a  
 319 threshold-based landscape measure.

320 **discuss better this point and see if we should keep it like that:**

321 Third, given that the estimation of  $\beta$  and  $\phi$  is independent, the most likely ZoI can differ significantly  
 322 between  $\phi_{nearest}$  and  $\phi_{cum}$ , depending on the abundance and spatial distribution of features. For private  
 323 cottages, which are present at high densities in our study area, the estimated ZoI for the cumulative influ-  
 324 ence was 10 km and the magnitude of the impact was small (Fig. C3). In contrast, if only the nearest feature  
 325 was considered, the estimated ZoI would be ten times lower (1 km) and the magnitude of the impact would  
 326 be several orders of magnitude higher. This was not the case for tourist cabins, however, which are scarce  
 327 and sparsely distributed in the study area (Fig. C4).

## 328 5.2 Assumption, advantages, and limitations of the approach

329 As formulated here, the influence of the nearest feature ( $\phi_{nearest}$ , eq. 3) and the cumulative influence  
 330 ( $\phi_{cum}$ , eq. 4) are calculated before model fitting through the `oneimpact` R package or through geo-  
 331 graphical information system tools. Here lies one of the main strengths of the approach: the cumulative  
 332 impacts of multiple features of an infrastructure are estimated through selection of models with either of  
 333 the influence measures, for instance through model performance measures (e.g. AIC or  $R^2$ ; Jackson &  
 334 Fahrig 2015; Huais 2018), without the necessity of repeated model fitting and complex parameterization  
 335 of non-linear functions (Lee *et al.*, 2020). This allows one to estimate the influence function and the ZoI  
 336 for several types of infrastructure. It also allows fitting models for large datasets (millions of points, e.g.  
 337 Tucker *et al.*, 2018) encompassing large study areas and fine resolution landscape covariates, what makes  
 338 the approach applicable over a wide range of fields in ecology. Furthermore, the pre-computation of  $\phi$   
 339 makes their visualization easy and their calculation computationally efficient and flexible.

340 Our formulation of the influence functions follow two main assumptions. First,  $\phi$  is assumed present a  
 341 constant ZoI, regardless of the density of points in an area. A possibly more reasonable assumption would  
 342 be to consider that the ZoI of a single of few features is smaller than that of a clusters of features, which  
 343 are expected to cumulatively affect a wider area. Analogous calculations with variable function size have  
 344 been implemented for decades in adaptive kernel density estimation [REF], so this premise can in principle

be relaxed. Second, our formulation represent two extremes where only the nearest feature influence a focal ecological process ( $\beta_i = 0$  for  $i > 1$ ) or all features affect the process equally ( $\beta$  is constant over all features). This is the simplest form of accounting for cumulative effects of multiple features of the same type. The advantage of this formulation lies on the independence between the magnitude of the impacts ( $\beta$ 's) and the influence functions ( $\phi$ ), what makes it possible to pre-compute  $\phi$  in GIS before model fitting. However, more complex formulations could be extended from eq. 2, for instance by considering that the influence of multiple features accumulate yet the closest one exerts a larger influence than features far away (higher  $\beta$  for the nearest feature).

Through simulations, we showed that  $\phi_{nearest}$  and  $\phi_{cum}$  represent similar gradients of spatial variation when the spatial distribution of infrastructure features is sparse and the ZoI is small (so that the features are too spaced for their effects to accumulate) and when the features are clustered and ZoI is large (in which case the clusters of features act as “super-features”, e.g. urban areas instead of houses; Appendix B). In these two situations, due to their correlation, one might be limited in distinguishing whether the impacts of multiple infrastructure on biodiversity accumulate. This might be assessed prior to statistical analysis through the computation of both influence measures at multiple ZoI and a careful evaluation of their correlations. However, as the “true” ZoI of an infrastructure type is hardly known in advance for any system, we recommend a general approach of computing and using the two influence measures, to test if there is evidence of cumulative impacts in the different ecological systems and processes.

It is important to remark that the extent of the study area and the zones of influence to be tested must be carefully selected, especially in cumulative impact assessment where the interplay between multiple factors may produce complex setups. First, the effects of infrastructure on ecological processes might differ depending of the extent of the study area (Vistnes & Nellemann, 2008). Skarin & Åhman (2014) showed that, depending of the temporal and spatial range of the study, the same type of infrastructure might vary in their effect to ecological variables, from no effect to positive or negative effects. As we show here, the spatial configuration of features and the ZoI might also affect our ability to detect if the impacts of infrastructure accumulate. Second, depending on the ecological response variable, the range of ZoI tested must encompass values much higher than the range size or even the average dispersal distance of an species (Jackson & Fahrig, 2012). If the ZoI values are not properly defined, the “true” ZoI at which the ecological process being measured is affected might not be selected, the resulting estimated ZoI might be wrong and mislead management and conservation policies based on that scientific inference (e.g. Jackson & Fahrig, 2015).



## 6 Conclusions

There is an increasing need to include cumulative impacts on environmental impact assessments and ecological studies. However, even when they are present, bringing concepts and theoretical frameworks into concrete and objective analyses to estimate cumulative impacts is often challenging and left to the responsibility of either the analysts or the regulators that review impact assessments (Johnson, 2011). Our approach offers resources to ecologists, environmental agencies, and stakeholders dealing with impact assessment to build concrete estimates of cumulative impacts of multiple features of an infrastructure and their zone influence. Even though the examples given here focused on animal space use, the cumulative influence measure we presented is applicable over a wide range of fields within ecology. Our formulation might be easily adapted to model other types of biological responses, such as population abundance (e.g. Benítez-López *et al.*, 2010), species richness (e.g. Ficetola & Denoël, 2009) or other measures of biological diversity and ecological processes REF[e.g.], with direct application in environmental and strategic impact assessment and integrated land use planning.

## Authors' contributions

BBN, BVM, and MP conceived the idea, designed the methods, and analyzed and discussed the data. BBN, BVM, MP, TT, KL, and OS provided data. BBN and BVM wrote the first draft. All authors contributed with discussions and to the final version of the manuscript.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data availability statement

GPS data is archived in Movebank ([www.movebank.org](http://www.movebank.org)) and might be accessed upon request. All environmental data was retrieved from public repositories. The `oneimpact` package is open and available at

401 `github.com/NINAnor/oneimpact`, and all scripts used in the analyses are available in the Github  
402 repository `github.com/bniebuhr/cumulative_influence_paper` (to be made public upon  
403 the acceptance of the manuscript).

## 404 **Supplementary Material**

405 Appendix A. Deriving the cumulative influence for line and polygon representations of infrastructure.  
406 Appendix B. Comparing the the influence of the nearest feature with the cumulative influence of multiple  
407 features  
408 Appendix C. Cumulative influence of infrastructure on reindeer space use: fitting habitat selection models  
409 Appendix D. Getting started with `oneimpact`.  
410 Appendix E. Calculating cumulative influence in GRASS GIS using the `oneimpact` package in R.

## 411 **References**

- 412 Bakkestuen, V., Erikstad, L. & Halvorsen, R. (2008) Step-less models for regional environmental variation  
413 in Norway. *Journal of Biogeography* **35**, 1906–1922.
- 414 Barber, C.P., Cochrane, M.A., Souza, C.M. & Laurance, W.F. (2014) Roads, deforestation, and the miti-  
415 gating effect of protected areas in the Amazon. *Biological Conservation* **177**, 203–209.
- 416 Benítez-López, A., Alkemade, R. & Verweij, P.A. (2010) The impacts of roads and other infrastructure on  
417 mammal and bird populations: A meta-analysis. *Biological Conservation* **143**, 1307–1316.
- 418 Boulanger, J., Poole, K.G., Gunn, A. & Wierzchowski, J. (2012) Estimating the zone of influence of  
419 industrial developments on wildlife: a migratory caribou *Rangifer tarandus groenlandicus* and diamond  
420 mine case study. *Wildlife Biology* **18**, 164–179.
- 421 Burnham, K.P., Anderson, D.R. & Burnham, K.P. (2002) *Model selection and multimodel inference: a*  
422 *practical information-theoretic approach*. Springer, New York, 2nd ed edn., oCLC: ocm48557578.
- 423 Ficetola, G.F. & Denoël, M. (2009) Ecological thresholds: an assessment of methods to identify abrupt  
424 changes in species–habitat relationships. *Ecography* **32**, 1075–1084.
- 425 Fieberg, J., Signer, J., Smith, B. & Avgar, T. (2021) A ‘How to’ guide for interpreting parameters in  
426 habitat-selection analyses. *Journal of Animal Ecology* **90**, 1027–1043.

- Gillingham, M.P., Halseth, G.R., Johnson, C.J. & Parkes, M.W. (eds.) (2016) *The Integration Imperative: cumulative environmental, community and health effects of multiple natural resource developments*. Springer International Publishing, Cham.
- GRASS Development Team (2017) *Geographic Resources Analysis Support System (GRASS GIS) Software, Version 7.8*. Open Source Geospatial Foundation.
- Huais, P.Y. (2018) multfit: an R function for multi-scale analysis in landscape ecology. *Landscape Ecology* **33**, 1023–1028.
- Ibisch, P.L., Hoffmann, M.T., Kreft, S., Pe’er, G., Kati, V., Biber-Freudenberger, L., DellaSala, D.A., Vale, M.M., Hobson, P.R. & Selva, N. (2016) A global map of roadless areas and their conservation status. *Science* **354**, 1423–1427.
- Jackson, H.B. & Fahrig, L. (2012) What size is a biologically relevant landscape? *Landscape Ecology* **27**, 929–941.
- Jackson, H.B. & Fahrig, L. (2015) Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography* **24**, 52–63.
- Johnson, C.J. (2011) Regulating and planning for cumulative effects: the Canadian experience. *Cumulative effects in wildlife management: impact mitigation* (eds. P.R. Krausman & L.K. Harris), pp. 29–46, CRC Press, Boca Raton, 1 edn.
- Johnson, C.J., Boyce, M.S., Case, R.L., Cluff, H.D., Gau, R.J., Gunn, A. & Mulders, R. (2005) Cumulative Effects of Human Developments on Arctic Wildlife. *WILDLIFE MONOGRAPHS* p. 36.
- Johnson, C.J. & St-Laurent, M.H. (2011) Unifying Framework for Understanding Impacts of Human Developments on Wildlife. *Energy Development and Wildlife Conservation in Western North America* (ed. D.E. Naugle), pp. 27–54, Island Press/Center for Resource Economics, Washington, DC.
- Laforge, M.P., Vander Wal, E., Brook, R.K., Bayne, E.M. & McLoughlin, P.D. (2015) Process-focussed, multi-grain resource selection functions. *Ecological Modelling* **305**, 10–21.
- Laurance, W.F. (2018) Conservation and the Global Infrastructure Tsunami: Disclose, Debate, Delay! *Trends in Ecology & Evolution* **33**, 568–571.
- Laurance, W.F. & Arrea, I.B. (2017) Roads to riches or ruin? *Science* **358**, 442–444.

- 454 Lee, Y., Alam, M., Sandström, P. & Skarin, A. (2020) Estimating zones of influence using threshold re-  
455 gression.
- 456 McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C. & Cushman, S.A. (2016) Multi-scale habitat selection  
457 modeling: a review and outlook. *Landscape Ecology* **31**, 1161–1175.
- 458 Miguet, P., Fahrig, L. & Lavigne, C. (2017) How to quantify a distance-dependent landscape effect on a  
459 biological response. *Methods in Ecology and Evolution* **8**, 1717–1724.
- 460 Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J.,  
461 Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feld-  
462 man, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V.,  
463 Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips,  
464 H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M.,  
465 Mace, G.M., Scharlemann, J.P.W. & Purvis, A. (2015) Global effects of land use on local terrestrial  
466 biodiversity. *Nature* **520**, 45–50.
- 467 Panzacchi, M., Van Moorter, B., Strand, O., Loe, L.E. & Reimers, E. (2015) Searching for the fundamental  
468 niche using individual-based habitat selection modelling across populations. *Ecography* **38**, 659–669.
- 469 Polfus, J., Hebblewhite, M. & Heinemeyer, K. (2011) Identifying indirect habitat loss and avoidance of  
470 human infrastructure by northern mountain woodland caribou. *Biological Conservation* **144**, 2637–2646.
- 471 Quiñonez-Piñón, R., Mendoza-Durán, A. & Valeo, C. (2007) Design of an environmental monitoring pro-  
472 gram using NDVI and cumulative effects assessment. *International Journal of Remote Sensing* **28**, 1643–  
473 1664.
- 474 R Core Team (2020) *R: A Language and Environment for Statistical Computing*. R Foundation for Statis-  
475 tical Computing, Vienna, Austria.
- 476 Skarin, A., Sandström, P. & Alam, M. (2018) Out of sight of wind turbines: Reindeer response to wind  
477 farms in operation. *Ecology and Evolution* **8**, 9906–9919.
- 478 Skarin, A. & Åhman, B. (2014) Do human activity and infrastructure disturb domesticated reindeer? The  
479 need for the reindeer’s perspective. *Polar Biology* **37**, 1041–1054.
- 480 Sloan, S., Jenkins, C.N., Joppa, L.N., Gaveau, D.L. & Laurance, W.F. (2014) Remaining natural vegetation  
481 in the global biodiversity hotspots. *Biological Conservation* **177**, 12–24.

- Thurfjell, H., Ciuti, S. & Boyce, M.S. (2014) Applications of step-selection functions in ecology and conservation. *Movement Ecology* **2**, 4.
- Torres, A., Jaeger, J.A.G. & Alonso, J.C. (2016) Assessing large-scale wildlife responses to human infrastructure development. *Proceedings of the National Academy of Sciences* **113**, 8472–8477.
- Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J.L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F.M., Blake, S., Blaum, N., Bracis, C., Brown, D., de Bruyn, P.J.N., Cagnacci, F., Calabrese, J.M., Camilo-Alves, C., Chamaillé-Jammes, S., Chiaradia, A., Davidson, S.C., Dennis, T., DeStefano, S., Diefenbach, D., Douglas-Hamilton, I., Fennessy, J., Fichtel, C., Fiedler, W., Fischer, C., Fischhoff, I., Fleming, C.H., Ford, A.T., Fritz, S.A., Gehr, B., Goheen, J.R., Gurarie, E., Hebblewhite, M., Heurich, M., Hewison, A.J.M., Hof, C., Hurme, E., Isbell, L.A., Janssen, R., Jeltsch, F., Kaczensky, P., Kane, A., Kappeler, P.M., Kauffman, M., Kays, R., Kimuyu, D., Koch, F., Kranstauber, B., LaPoint, S., Leimgruber, P., Linnell, J.D.C., López-López, P., Markham, A.C., Mattisson, J., Medici, E.P., Mellone, U., Merrill, E., de Miranda Mourão, G., Morato, R.G., Morellet, N., Morrison, T.A., Díaz-Muñoz, S.L., Mysterud, A., Nandintsetseg, D., Nathan, R., Niamir, A., Odden, J., O'Hara, R.B., Oliveira-Santos, L.G.R., Olson, K.A., Patterson, B.D., Cunha de Paula, R., Pedrotti, L., Reineking, B., Rimmler, M., Rogers, T.L., Rolandsen, C.M., Rosenberry, C.S., Rubenstein, D.I., Safi, K., Saïd, S., Sapir, N., Sawyer, H., Schmidt, N.M., Selva, N., Sergiel, A., Shiilegdamba, E., Silva, J.P., Singh, N., Solberg, E.J., Spiegel, O., Strand, O., Sundaresan, S., Ullmann, W., Voigt, U., Wall, J., Wattles, D., Wikelski, M., Wilmers, C.C., Wilson, J.W., Wittemyer, G., Zieba, F., Zwijacz-Kozica, T. & Mueller, T. (2018) Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* **359**, 466–469.
- Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A. & Watson, J.E.M. (2016) Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications* **7**, 12558.
- Vistnes, I. & Nellemann, C. (2008) The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. *Polar Biology* **31**, 399–407.
- Zeller, K.A., Vickers, T.W., Ernest, H.B. & Boyce, W.M. (2017) Multi-level, multi-scale resource selection functions and resistance surfaces for conservation planning: Pumas as a case study. *PLOS ONE* **12**, e0179570.

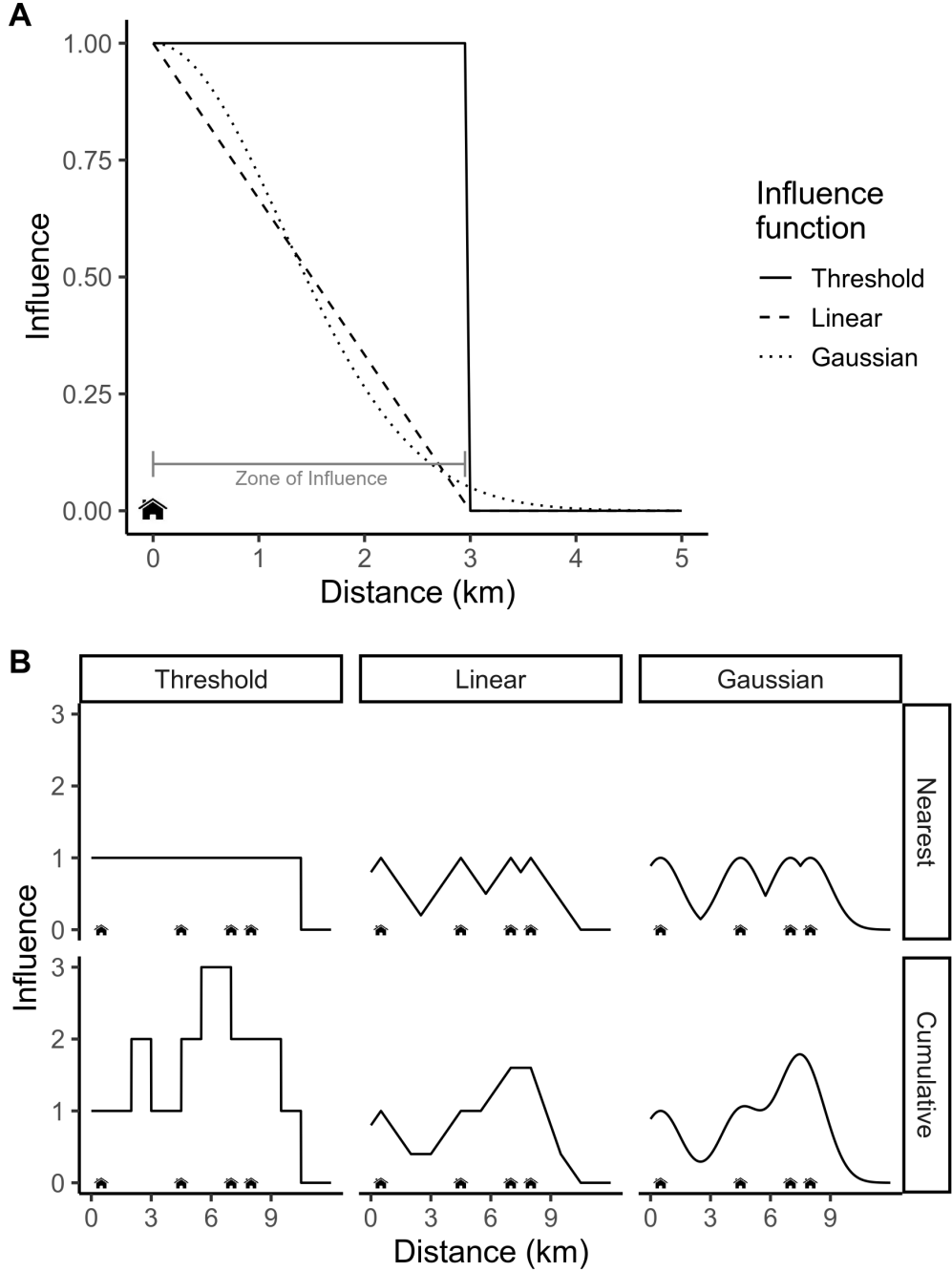


Figure 1: Illustration of the influence ( $\phi_{i_k}$ ) of infrastructure features against the distance from those features ( $d_{i_k}$ ), simplified for one dimension and using houses as an example. (A) Examples of influence functions according which the influence of the house might vary. A house has only an influence within its zone of influence (here  $ZoI_{i_k} = 3$  km). For the threshold function, the influence remains constant within the ZoI and drops to zero beyond it, whereas for both the linear and Gaussian functions it declines monotonically within the ZoI. For functions that asymptotically approach zero, a cutoff must be selected to characterize the ZoI (here the ZoI is the distance where the influence decreases to  $\phi_{i_k} < 0.05$ ). (B) Representation of the influence of multiple houses by considering only the nearest feature (upper row) or the cumulative influence of multiple features (bottom row), for different influence functions. If only the nearest house is considered, the influence does not exceed one; when all houses act cumulatively, their cumulative influence can be much higher than one.

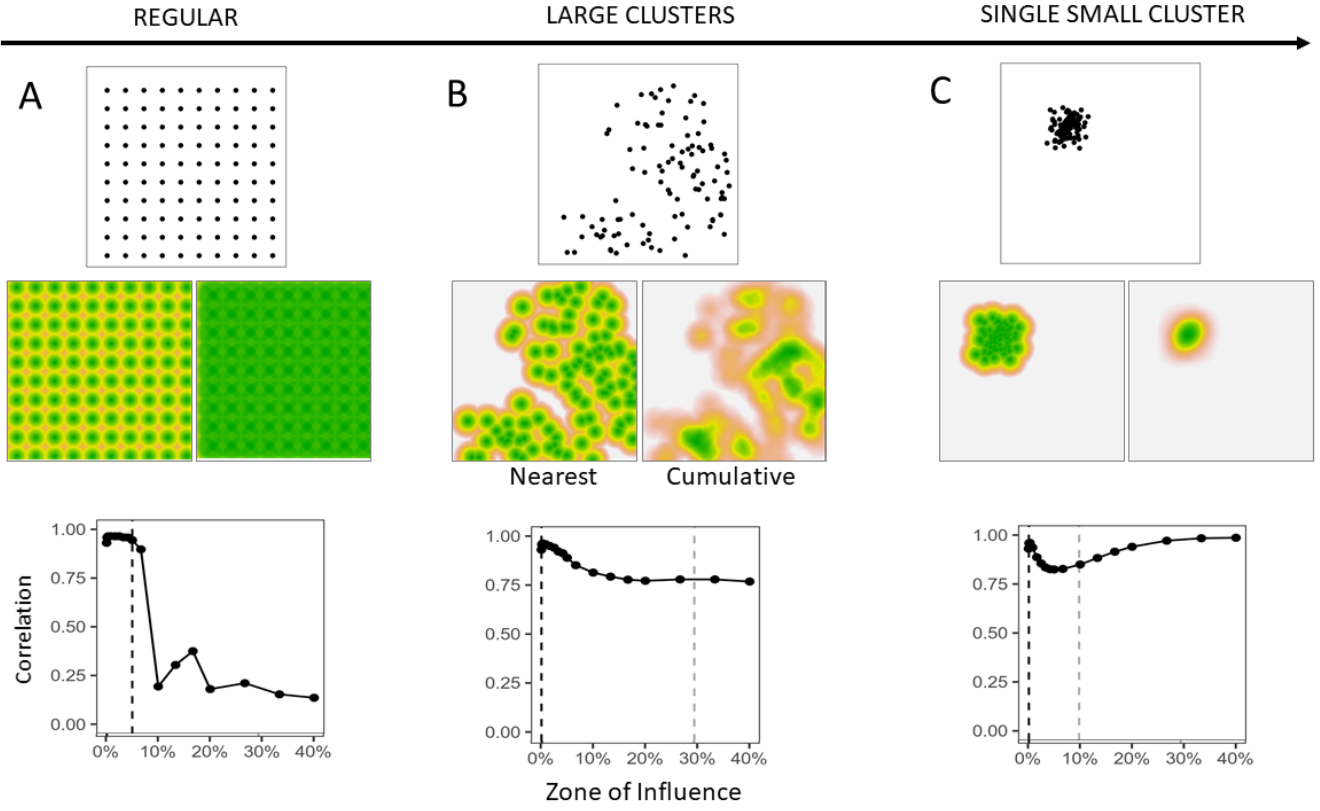


Figure 2: Representation of the influence of nearest feature ( $\phi_{nearest}$ ) and the cumulative influence ( $\phi_{cum}$ ) in landscapes with point infrastructure spatially distributed in a gradient of clustering, from (A) a regular distribution to (B) a set of clusters to (C) only one cluster. The central panel shows a visual comparison between  $\phi_{nearest}$  (left) and  $\phi_{cum}$  (right) when ZoI is 10% of the landscape extent. The lower panel shows the correlation between  $\phi_{nearest}$  and  $\phi_{nearest}$  in each landscape, as their ZoI increases. The dashed vertical lines show half the the minimum distance between features (black), beyond which there are cumulative effects of the different infrastructure, and the size of the feature clusters (grey), beyond which the correlation stops decreasing.

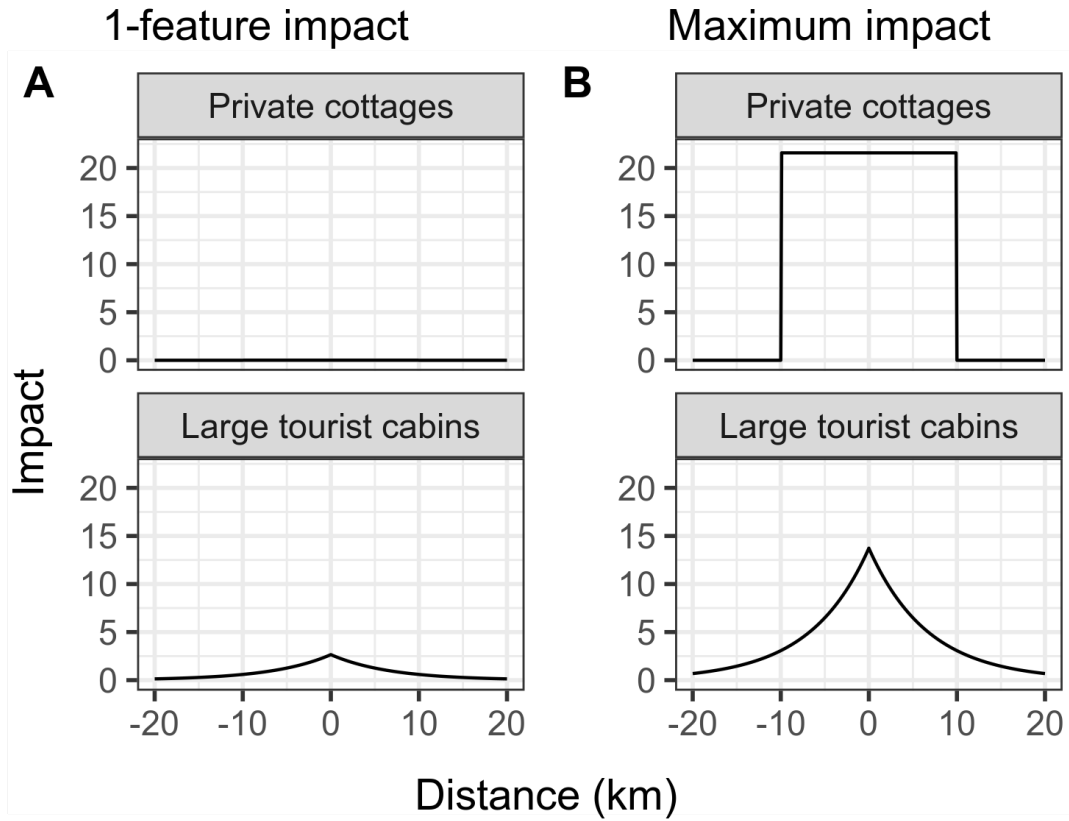


Figure 3: Impact of private cottages and public cabins considering (A) only 1 feature and (B) the maximum number of features of each type of infrastructure in the study area (2664 for cottages, 5 for cabins). The impact is the multiplication between the magnitude of the impact (model coefficients) and the cumulative influence function ( $\phi_{cum}$ ). While the impact of only one private cottage is negligible, at their maximum densities the cumulative impact of private cottages is higher than that of tourist cabins.



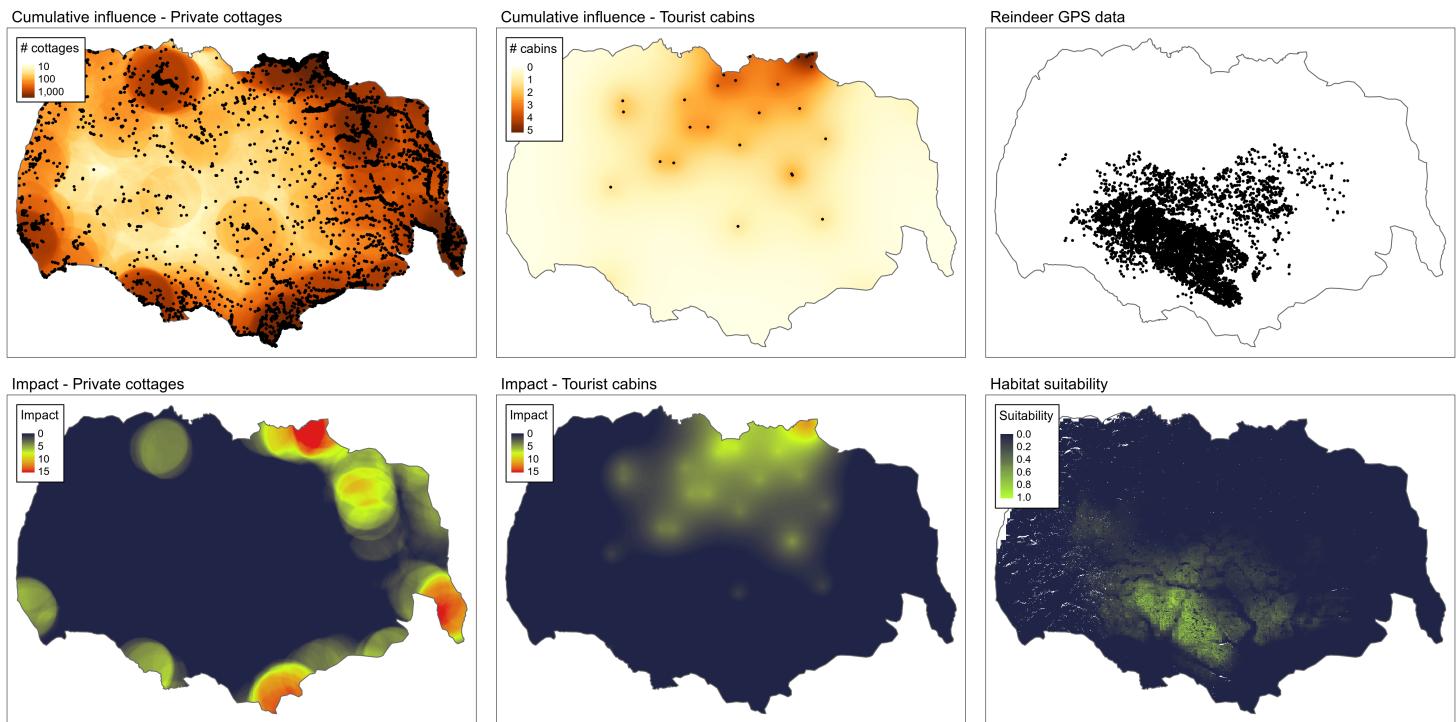


Figure 4: Maps of the most parsimonious cumulative influence variables (private cottages: threshold with 10km ZoI; tourist cabins: exponential decay with 20 km ZoI) and their estimated impacts on reindeer habitat selection. These maps are shown alongside the reindeer GPS locations in the Hardengervidda wild reindeer area and the estimated reindeer habitat suitability.