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ANALYSIS OF THE HUMAN FOOTPRINT ON REINDEER SUMMER HABITAT

Using habitat selection modeling to assess anthropogenic drivers of habitat loss in Norwegian wild mountain reindeer (*Rangifer tarandus tarandus*)

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ABSTRACT

1. Of particular importance to wildlife conservation and mitigation of the current biodiversity crisis are questions of habitat loss and degradation. In this context, disturbance studies have sought to implement new methods for studying wildlife populations in relation to their environment when subjected to the human footprint. Habitat selection models have proven to be powerful tools for quantifying the impact of human disturbances on wildlife habitat and estimating disturbance parameters influencing spatial and temporal distribution of a species from occurrence data.

2. During the last century, Norway has experienced fast-paced infrastructure development that has resulted in the massive loss of mountain wilderness. In those same mountains live the last remaining populations of wild mountain reindeer (*Rangifer tarandus tarandus*) in Europe. With pervasive human influence and multiple claims placed on Norwegian mountains, seasonal habitat loss is currently suggested as the main threat for wild reindeer in southern Norway. Accordingly, the Norwegian Government is investing considerable resources into habitat loss assessment, as a critical step to determine if these areas will be able to support viable population units in the future.

3. With the purpose to unravel and quantify the drivers of anthropogenic habitat loss in wild reindeer summer habitat, the present research investigated reindeer habitat use on summer ranges in relation to the human footprint in southern Norway, using existing resource selection functions (RSFs), developed for wild reindeer, and GPS data. Overall, human disturbances were found to induce substantial habitat loss (> 50%) in wild reindeer summer ranges. However, differences could be noted between herds, both in relation to the uneven spatial distribution of the human footprint and the main drivers of anthropogenic habitat loss, which were found to vary between reindeer areas. For the study area as a whole, highest avoidance levels during summertime were induced by the grazing animals from domestic livestock, primarily, as well as by houses of the domestic sector, low traffic summer roads and hiking trails.

4. The present human footprint analysis points out the need for prioritized management and targeted mitigation of herd-specific disturbance sources in wild reindeer ranges. Moreover, it provides key insights for the future prevention of human-reindeer conflicts and will hopefully help to balance wild reindeer conservation with anthropogenic development. This study and the approach it proposes may provide a valuable framework for quantifying the impacts of the human footprint in further biodiversity components, and thus help tackle the loss of natural habitats.

RÉSUMÉ

1. Les questions de perte et de dégradation des habitats revêtent une importance capitale pour la conservation de la faune sauvage et l'atténuation de la crise actuelle de la biodiversité. Dans ce contexte, les études relatives aux perturbations anthropiques de la faune sauvage ont cherché à mettre en œuvre de nouvelles méthodes pour étudier les relations entre les populations animales et leur environnement lorsqu'il est soumis à l'empreinte humaine. Les modèles de sélection de l'habitat ont émergé comme des outils puissants pour quantifier l'impact des perturbations humaines sur l'habitat des espèces et estimer les paramètres de perturbation influençant la distribution spatiale et temporelle de ces dernières à partir de données d'occurrence.

2. Au cours du siècle dernier, la Norvège a connu un développement rapide des infrastructures qui a entraîné la disparition massive d'habitats sauvages dans les montagnes, là où vivent les dernières populations de renne sauvage (*Rangifer tarandus tarandus*) d'Europe. Compte tenu de l'influence omniprésente de l'homme et des multiples revendications qui pèsent sur les paysages montagneux norvégiens, la perte d'habitat saisonnier est actuellement considérée comme la principale menace pour le renne sauvage dans le sud de la Norvège. En conséquence, le gouvernement norvégien consacre des ressources considérables à l'évaluation de la perte d'habitat, une étape essentielle pour déterminer si ces régions seront en mesure d'accueillir des unités de population viables à l'avenir.

3. Dans le but de déterminer et de quantifier les principaux facteurs de perte d'habitat anthropique dans les aires estivales du renne sauvage, la présente étude a examiné l'utilisation de l'habitat faite par l'espèce en relation avec l'empreinte humaine durant cette saison, en utilisant des modèles de sélection de l'habitat (RSFs) existants, développés pour le renne sauvage, et des données GPS. Globalement, il a été constaté que les perturbations humaines induisaient une perte d'habitat importante ($> 50\,\%$) dans la majorité des aires d'estivage. Cependant, des différences ont pu être constatées entre les hardes en ce qui concerne la distribution spatiale de l'empreinte humaine et les principaux facteurs de perte d'habitat anthropique, qui se sont avérés varier entre les régions. Pour l'ensemble de la zone d'étude, la perte d'habitat estival fut principalement causée par le bétail domestique, ainsi que les maisons, les routes à faible trafic et les sentiers de randonnée.

4. La présente analyse de l'empreinte humaine souligne la nécessité d'une gestion hiérarchisée et d'une atténuation ciblée des perturbations humaines dans l'habitat du renne. En outre, elle fournit des indications essentielles pour la prévention future des conflits entre l'homme et le renne, et permettra, espérons-le, de concilier conservation du renne sauvage et développement anthropique. Cette étude, et l'approche qu'elle propose, devraient fournir un cadre utile pour quantifier l'impact de l'empreinte humaine chez d'autres espèces, et ainsi aider à lutter contre la perte d'habitats.

LIST OF ABBREVIATIONS

AIC	Akaike Information Criterion
EIA	Environmental Impact Assessment
GIS	Geographic Information System
GPS	Global Positioning System
HFP	Human footprint
NDVI	Normalized Difference Vegetation Index
NORUT	Northern Research Institute
QN	Quality Norm
QN3A	Quality norm criterion on the loss of seasonal habitat
RSF	Resource Selection Function
TUI	Trail Use Index
TPI	Topographic Position Index
ZOI	Zone of influence

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INTRODUCTION

1. <u>Anthropogenic development and its impacts on wildlife habitat</u>

As we move through the Anthropocene, humans are putting nature under great pressure and causing unprecedented changes to ecosystems (Corlett, 2015). Largely driven by global population growth and associated industrial development, recent centuries have seen significant land-use changes and rapid expansion of infrastructure across landscapes (UNEP, 2001). The terrestrial human footprint has expanded spatially (Venter et al., 2016a), and fast-paced encroachment on wildlands has led more than 80% of the Earth's land surface being exposed to human activities (Watson & Venter, 2019). Alongside climate change, overexploitation and spread of invasive species, land-use changes are among the main drivers affecting global ecosystems (WWF, 2020). Unbridled anthropogenic development is profoundly changing landscapes, disrupting species interactions with their habitat and altering ecosystem functioning (Newbold et al., 2015; Trombulak & Frissell, 2000). In particular, human activity and infrastructure have substantially impaired natural habitats and reduced their carrying capacity to a significant extent (Díaz et al., 2019; Krausman & Harris, 2011). Adverse effects on wildlife populations in the vicinity of human developments have been studied for decades and are now widely acknowledged (Benítez-López et al., 2010), with documented changes induced in species distribution, abundance and persistence (Johnson & St-Laurent, 2011). Indeed, habitat loss and fragmentation have emerged as the major threats to terrestrial wildlife, becoming the leading causes of species extinction and biodiversity loss worldwide (Brooks et al., 2002; Gu et al., 2004).

Maintaining sustainable wildlife populations in our present-day, human-dominated landscapes is one of the greatest challenges of modern conservation. Therefore, reducing human-wildlife conflicts has become a major priority in disturbance research (Sutherland et al., 2006; Treves et al., 2006). This concern is all the more relevant since the trend towards anthropogenic development is not projected to reverse, with an ever-increasing demand for space and resource consumption expected in the years to come (Tilman et al., 2002; UNEP, 2001). With many wildlife populations facing decline, understanding how human-induced landscape changes affect species habitat is a paramount requirement to sustainably manage these populations and their habitat (Lindenmayer et al., 2008; Turner et al., 2007).

2. <u>Changing trends in environmental impact assessment</u>

Concretely, this context has brought out the need to further investigate wildlife responses to human disturbance (Sutherland, 2007), what subsequently led the field of environmental impact assessment (EIA) to develop, with a pivotal role to play in the reduction of human-wildlife conflicts (Treweek, 2009). EIA encompasses many procedural tools and techniques meant to understand, monitor and quantify human-induced impact schemes ecosystems are subjected to (Bai & Bai, 2014; Bidstrup et al., 2016). Aimed at developing the ability for predicting and anticipating ecological implications of proposed developments or policies, the EIA process is intended to improve the mitigation of anthropogenic impacts by supporting informed decisions towards long-term conservation and sustainable land-use planning (Hill & Arnold, 2012; Treweek, 2009). In particular, mitigation of infrastructure development and anthropogenic land-use changes requires a thorough understanding of species response to anthropogenic disturbance and related consequences for their populations (Treves et al., 2006). However, studying future anthropogenic landscape changes and predicting their consequences on wildlife populations and species habitat is not a straightforward process (MacDonald, 2000). Early EIA approaches and disturbance studies have traditionally focused on single stressors, mostly investigating direct, short-term and small-scale responses to human disturbance at the individual level (Hill & Arnold, 2012; Kennett, 1999; Schultz, 2010; Vistnes & Nellemann, 2008). Yet, there is increasing evidence supporting the existence of complex interactions between anthropogenic stressors, leading their adverse effects to combine, accumulate and result in a cumulative impact that is significantly greater than that of each disturbance source considered separately (Burton et al., 2014; Foley et al., 2005; Geldmann et al., 2014). Repeated risk exposure and resulting avoidance response built up over space and time, and integrated for all types of disturbances, may thus result in considerable cumulative impacts, notably in terms of habitat loss (Johnson & St-Laurent, 2011; Wang et al., 2014).

So-called cumulative impacts can be defined as '[…] the outcomes of multiple land-use practices or developments that aggregate over time and space' (Johnson & St-Laurent, 2011). This phenomenon is also discussed through the concept of 'nibbling' or 'piecemeal development', where many incremental, additional changes result in a large cumulative impact (Krausman & Harris, 2011; Nellemann et al., 2003a; Sorensen et al., 2010; Vistnes et al., 2001). It has therefore become fundamental to modern ecology that assessing the impact of human disturbances without paying adequate attention to their aggregate effect critically underestimates the cumulative, long-

term and large-scale impacts resulting from the entire network of activities and infrastructures affecting landscapes (Burton et al., 2014; Duinker & Greig, 2006; Kennett, 1999). Thus, largely driven by the emerging awareness on the importance of cumulative impacts for landscape management and conservation planning (Tulloch et al., 2015), the field of EIA has progressively shifted in scale and focus over the past decades (Duinker & Greig, 2006; Kennett, 1999). More recent disturbance studies increasingly tend to consider broader spatio-temporal contexts and document changes in population processes or landscape functioning (Krausman & Harris, 2011; Nitschke, 2008; Schultz, 2010; Toews et al., 2018; Vistnes & Nellemann, 2008). These changes have greatly enhanced the likelihood of detecting impacts and the ability to evaluate disturbance effects at scales of higher relevance for management (Schultz, 2010; Vistnes & Nellemann, 2008). Moving towards a more comprehensive and holistic approach, EIA started considering cumulative impacts assessment as an essential requirement for complete and reliable environmental management (see e.g., Bidstrup et al., 2016; Burton et al., 2014; Duinker & Greig, 2006; Johnson et al., 2010; Theobald et al., 1997). Notwithstanding the fact that early EIA approaches helped in building fundamental knowledge, it is now widely agreed these are insufficient for efficiently tracking cumulative impact schemes and untangling large-scale, complex disturbance patterns, thus leading to significant underestimations (Duinker & Greig, 2006; Lindenmayer et al., 2008). Current recommendations in EIA call for multi-scale disturbance research, with a focus on regional and cumulative impacts, in order to build a body of knowledge that fully describes the range of anthropogenic effects ecosystems are subjected to (Lindenmayer et al., 2008; Sutherland, 2007).

3. <u>Monitoring anthropogenic pressures through the human footprint</u>

To achieve sustainable development and ensure effective wildlife conservation, it is critical to monitor human pressures on ecosystems (Di Marco et al., 2018). The human footprint (HFP) is a central concept that has progressively gained prominence for detecting, monitoring and representing the continuum of anthropogenic pressures on the terrestrial environment (Mora & Zapata, 2011; Sanderson et al., 2002; Watson & Venter, 2019). In particular, the HFP conceptual framework has widely served to map the global distribution of anthropogenic impacts and track their changes over space and time (see Venter et al., 2016a, 2016b), while simultaneously providing information on the wilderness status of landscapes and potential conservation locations (Hirsh-Pearson et al., 2021; Rosas et al., 2021; Williams et al., 2020). Closely related to the concept of cumulative impacts, the HFP furthermore provides a spatially explicit and time-consistent index

among the most popular to visualize and quantify the aggregated effects of multiple threats on terrestrial ecosystems (McGowan, 2016; Tapia-Armijos et al., 2017; Venter et al., 2016a; WWF, 2020). As such, the HFP represents a powerful tool to monitor the status of landscapes (Haines et al., 2008), which has found many applications in land-use planning, conservation and resource management (see e.g., Di Marco et al., 2018; Hill et al., 2020; Photopoulou, 2018; Rosas et al., 2021; Van der Marel et al., 2020).

Direct effects of the HFP include habitat loss due to infrastructural development and associated disturbance (Burton et al., 2014; Hand et al., 2014). Habitat loss can be defined as 'the temporary or permanent conversion of a habitat favorable to a species into an altered state of functional unsuitability for the maintenance of its populations' (Kerr & Cihlar, 2004; Mora & Zapata, 2011). Besides being a primary driver of wildlife population declines (Foley et al., 2005), habitat loss is also known to be highly predictive of species endangerment (Di Marco et al., 2018; Kerr & Cihlar, 2004). Therefore, quantifying and locating habitat loss induced by anthropogenic developments is critical to mitigate it and preserve landscapes and species habitat (Haines et al., 2008). In this regard, the HFP provides a very useful conceptual framework to anthropogenic habitat loss assessment. At its simplest, the HFP represents the spatial extent of a development and expresses its structural impact on habitat, i.e. the direct habitat loss caused by the conversion of native habitat to infrastructure (Sanderson et al., 2002). Yet, habitat loss is not limited to the physical extent of a development and is likely to extend beyond the structural footprint, by means of avoidance resulting from the disturbance this feature induces in wildlife (Benítez-López et al., 2010; Jalkotzy et al., 1997; Sawyer et al., 2006). Therefore, knowledge on species sensitivity and ecological response to human developments is crucial to provide insight into the functional implications of the HFP (Legendre et al., 2002; Toews et al., 2018). Avoidance responses to anthropogenic disturbances are typically modeled through an effect size and a zone of influence, which describe the strength and extent of habitat-use reduction (or loss) resulting from avoidance in the vicinity of a disturbance source (Boulanger et al., 2012; Polfus et al., 2011; Rettie, 2019). Such parameters largely depend on the species and stressors, as the avoidance response may be highly variable (Toews et al., 2018). Integrating the structural footprint in a functional background based on animal response to human disturbance is therefore essential to account for related habitat loss (Hill & Arnold, 2012; Polfus et al., 2011) and properly assess the actual ecological area affected by human developments (Legendre et al., 2002; Leu et al., 2008; Tattersall, 2019).

4. Habitat selection modeling and resource selection functions

Several methodological approaches exist for EIA. The choice of an appropriate assessment method largely depends on the ecosystem component being studied and the availability of data. In particular, disturbance studies can greatly vary in methodology (Flydal et al., 2019). Habitat selection models have become a common approach to estimate disturbance parameters influencing the spatial and temporal distribution of species from occurrence data (Bennett et al., 2009; Fieberg et al., 2018). Habitat selection is a fundamental ecological process through which animal chooses a certain location rather than another across the landscape, while all being offered on an equal basis, thus leading habitat to be unevenly used with respect to its availability (Alldredge & Griswold, 2006; Fretwell & Lucas, 1969). Early driven by the constant need to adapt to naturally changing environment, distribution dynamics were later substantially influenced and disturbed by human-induced landscape changes (WWF, 2020). In this context, Frid and Dill (2002) provide a very valuable framework for conceptualizing nonlethal human disturbance and its impacts on wildlife space use, wherein disturbance is approached as a form of predation risk, inducing avoidance and changes in habitat selection as for the antipredator behavior outlined in the so-called 'landscape of fear' (Hebblewhite & Merrill, 2008; Laundre et al., 2010; White & Gregovich, 2017). Therefore, the study of species habitat selection and resource use in human-disturbed landscapes provides critical insights for understanding how multiple disturbance sources can affect wildlife populations over space and time, as well as substantial guidance on appropriate management strategies to address them (Aarts et al., 2008; Northrup et al., 2015; White & Gregovich, 2017).

Technological advances and increasing reliance on Global Positioning Systems (GPS), radio-telemetry, and Geographic Information Systems (GIS) have led resource selection functions (RSFs) to gain popularity and widespread application in habitat selection studies (Northrup et al., 2013; Plante et al., 2018). Selection function modeling is a statistical process that quantifies relative resource use and assesses the influence of environmental variables on habitat selection in mobile, free-ranging species (McLoughlin et al., 2010). These models integrate information on animal location, such as GPS tracking data, together with remote sensing data on habitat variables in GIS, to be fitted in a 'use versus availability' design (Boyce et al., 2002; Johnson et al., 2006; Manly et al., 2002). The comparison of used and available locations – randomly sampled in the vicinity of used locations – in environmental space then allows for the identification of discriminant variables that are ecologically significant as drivers of habitat selection (Bouyer, 2015; Fieberg et al., 2018;

Johnson, 1980), and so likely to predict habitat use in the studied species (Boyce, 2006; Manly et al., 2002). Model predictions are proportional to the relative probability of use of a resource unit according to its habitat conditions, both natural and anthropogenic. As a result of resource selection modeling, the probability of use can be modeled across the landscape and used as a predictor of animal habitat selection (Arthur et al., 1996; Keating, 2009; McLoughlin et al., 2010). Based on the ecological theory that individuals select habitat to maximize their fitness, such models assume animal distribution somehow reflects the ecological requirements, preferences and tolerances of the studied species (Fahrig, 2001; Franklin & Miller, 2010).

Selection functions thus provide a robust framework for studying space use patterns in wildlife populations (Mcdonald & Manly, 2001), as well as a powerful template for describing the distribution of critical habitat and assessing anthropogenic habitat loss (Mcdonald & Mcdonald, 2002; Northrup et al., 2015; Sawyer et al., 2006). Such modeling methods have found many uses in modern conservation, land-use planning and resource management, where they are used to investigate various ecological questions and address important conservation issues, including cumulative impacts assessment. In disturbance studies, RSFs offer a valuable opportunity to quantify the avoidance response induced in wildlife populations (see e.g., Beckmann et al., 2012; Bennett et al., 2009; Johnson et al., 2004; Northrup et al., 2015; Polfus et al., 2011; White & Gregovich, 2017). Since the relative probability of use provided by selection functions can be interpreted as a proxy of habitat quality (Gaillard et al., 2010), investigating habitat use in the vicinity of human disturbance sources through RSFs constitutes a robust approach to assess anthropogenic habitat loss (Mcdonald & Mcdonald, 2002; Northrup et al., 2015). Furthermore, besides providing a strong methodology for quantitative assessment, the asset of RSF-type models lies in the use of species-specific, empirically derived disturbance parameters, what strengthen the ecological relevance and predictive power of related assessments (Boyce et al., 2002; Saura & Pascual-Hortal, 2007). In this thesis, selection functions were used to assess habitat quality and quantify anthropogenic habitat loss resulting from human infrastructure and activity.

5. *Rangifer tarandus* in the face of anthropogenic disturbance

The focus of this thesis is on the alpine tundra habitat, and more specifically, on its flagship species: *Rangifer tarandus*. Reindeer and caribou (both *Rangifer tarandus*) are circumpolar ungulates living over much of the Eurasian and North American Arctic (Forbes & Kumpula, 2009) (Fig. 1). The wide geographical extent of *Rangifer tarandus'* distribution range makes it home to many subspecies and ecotypes that occur in various habitats among the alpine, subarctic, arctic and boreal ecosystems (Bernes et al., 2015; Wilson & Reeder, 2005). Nevertheless, these remain broadly similar in their baseline ecology, being all highly mobile, herd-living and wide-ranging animals (Klein, 1996; Skogland, 1989). Herds, ranging in size from a few dozen up to thousands of individuals, typically spend winter in areas with relatively low snow cover and good supply in lichen, which reindeer mainly feed on during this season (Danell et al., 1994; Thomas & Hervieux, 1986). By the end of winter, they move to highly-productive, insect-free and low-predation sites to calve and spend summer (Mårell & Edenius, 2006). Calving occurs in spring and it usually takes place in elevated areas with sparse vegetation, selected by females to avoid predation (Bergerud et al., 1990). Bull groups head in outer areas to join early-fertile summer grazing grounds (Metsaranta & Mallory, 2007). Due to the short season of emergent green vegetation in the Arctic, summer is a pivotal period for reindeer growth and body condition (Skogland, 1984). High-quality, nutritive and protein-rich forage is required during summer, since high nutritional intake is essential for reindeer to recover from the winter energetic stress (Parker et al., 2009), as well as for meeting increased requirements occurring in both males and females, related to the pre-rute season for the former (Barboza et al., 2004), and the lactation period for the latter (Gerhart et al., 1997). Seasonal ranges can be more or less scattered and spatially distant depending on *Rangifer* subspecies (Festa-Bianchet et al., 2011). As a result, most populations yearly undertake seasonal migrations between their winter and summer grazing grounds (Berger, 2004), which comes in addition to daily smaller-scale movements within these ranges (Bernes et al., 2015). Given the dynamic nature of boreal ecosystems, *Rangifer tarandus* has adapted to natural disturbance regimes by making movement a key component of its ecology (Johnson et al., 2001; Schaefer & Mahoney, 2013). Migration has been operating for millennia (Berger et al., 2006), primarily to cope with spatio-temporal variations in forage distribution and limit predation (Bergerud & Page, 1987; Flydal et al., 2019; Fryxell & Sinclair, 1988; Rettie & Messier, 2000). The direct prerequisites of such a high mobility are large and continuous home ranges of hundreds to several hundred thousands of km² (Klein, 1996).
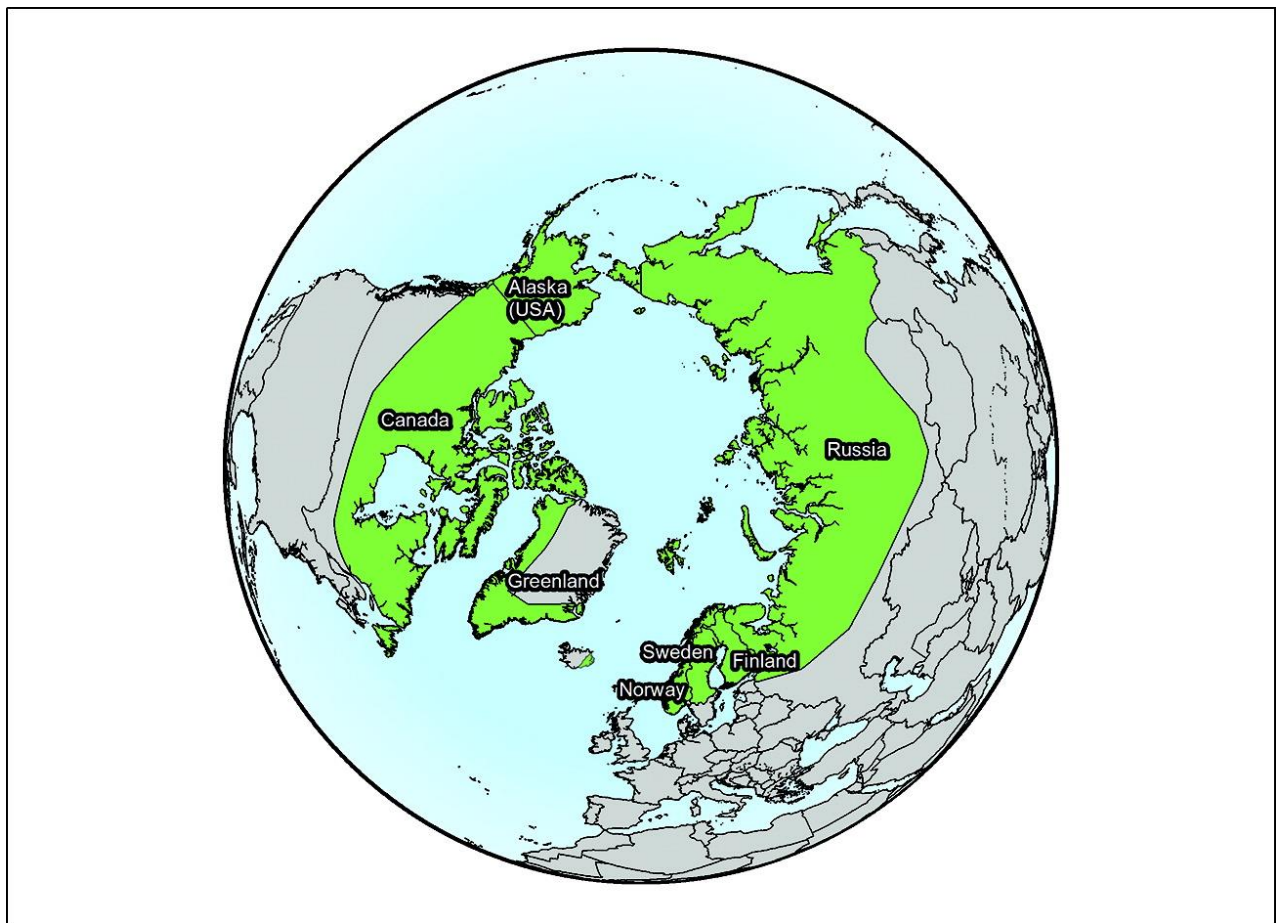
Figure 1
Global distribution of *Rangifer tarandus* (Mallory & Boyce, 2017).

Among large-size northern mammals, wild reindeer and caribou are particularly sensitive to humans and avoid most forms of anthropogenic disturbance (Benítez-López et al., 2010), with many studies documenting negative effects on foraging behavior, distribution, movement patterns and population dynamics (see Bergerud et al., 1984; Dyer et al., 2001; Flydal et al., 2019; Nellemann & Cameron, 1996; Vistnes et al., 2004; Wolfe et al., 2000). Because of large spatial requirements for continuous ranges, *Rangifer tarandus* is a very challenging species to conserve in our modern-day landscapes faced with habitat loss and fragmentation. Significant threats associated with human activities (e.g., forestry, tourism, energy production, transportation, etc.) and related infrastructures (e.g., roads, trails, houses, windparks, etc.) exist throughout the distribution range of the species, resulting in decreasing size of habitat patches and reduced connectivity (Falldorf, 2013; Plante, 2020) which are largely suggested to contribute to the decline of reindeer and caribou in northern regions around the world (Vors & Boyce, 2009). Accordingly,

several research have investigated *Rangifer* responses to human disturbances in the past decades (see Reimers & Colman, 2006; Vistnes & Nellemann, 2008; Wolfe et al., 2000 for reviews). While in many cases, specific knowledge is still lacking to adequately predict and mitigate conflicts with humans, anthropogenic landscape features are mainly known to interfere with two ecological process in *Rangifer tarandus*, namely range use and movement (Beyer et al., 2016; Vistnes et al., 2004). These effects operate through various mechanisms including habitat loss and fragmentation, and often result in a suite of ecological consequences (Toews et al., 2018). Proximity avoidance is typically observed in the species when facing human disturbance, which implies that reindeer may be found in disturbed areas, but with great reduction in their use of such locations (Johnson et al., 2010; Vistnes et al., 2001). This behavioral response is then likely to prevent animals from accessing suitable habitats and maintaining synchronicity with vegetation, while leading to frequent overgrazing in remaining pastures (Beauchesne et al., 2014; Dahle et al., 2008; Flydal et al., 2019; Fullman et al., 2021; Vistnes et al., 2004). Disturbance can also disrupt migration routes and movement rates in reindeer and caribou (Panzacchi et al., 2016, 2013a; Tucker et al., 2018; Vistnes et al., 2004), including delayed crossing of linear infrastructures (i.e., roads, trails, seismic lines, railways, pipelines, etc.) (Wilson et al., 2016). The potential costs of avoidance therefore include increased predation risk, reduced feeding time and interference with energy budget (Bergerud et al., 1984; Bradshaw et al., 1997; Frid & Dill, 2002; Plante, 2020), which may in turn affect species overall fitness and population performances through impaired body condition, reproductive and survival functions (Cameron et al., 2005; Losier et al., 2015; Vistnes et al., 2001; Weir et al., 2007).

The extent of these effects is furthermore prone to seasonality, sex-dependence, and may also vary according to several parameters such as the type of disturbance, the size of the herd or the combination with other stressors (Polfus et al., 2011; Vistnes & Nellemann, 2008). Although reindeer and caribou respond to human disturbance in all seasons, pre-calving and calving times are reported to be periods of higher sensitivity in the species (Dyer et al., 2001). Conversely, avoidance response tends to decrease when animals are faced with other stresses, such as insect-harassment in summer (Pollard et al., 1996; Skarin et al., 2004), or intense intra-specific interactions during the rutting season (Reimers & Colman, 2006). Maternal females and newborn calves are the most prone to disturbance among the population, avoiding human features in a broader extent (Cronin et al., 1998). Conversely, males and yearlings tend to be less reclusive and

more tolerant to close infrastructure (Nellemann & Cameron, 1996). Response to human disturbance can also vary in intensity depending on the size of the group, with larger herds being more responsive to disturbance than smaller ones (Nellemann et al., 2003; Nellemann et al., 2000). Finally, some studies report a positive relationship between avoidance behavior and novelty, thereby suggesting a potential for habituation in some particular cases (see Vistnes & Nellemann, 2008 for a discussion). In all instances, the strength and extent of the avoidance response remain proper to the type of disturbance, depending on its spatial extent and configuration, human traffic, and correlation with other disturbances (Vistnes et al., 2004; Vistnes & Nellemann, 2008). As being widely distributed among the globe, *Rangifer* populations are faced with various disturbance sources and drivers of habitat loss (Mallory & Boyce, 2017). Therefore, cumulative, regional-scaled and long-term studies are required to ensure assessment accuracy when studying the impacts of human activity and infrastructure in reindeer and caribou (Weir et al., 2007).

6. <u>The case of the Norwegian wild mountain reindeer</u>

This thesis focusses on Norwegian wild mountain reindeer (*Rangifer tarandus tarandus*), ranging in southern country. During the last century, Norway has experienced fast-paced infrastructure development that has resulted in a massive loss of mountain wilderness (UNEP, 2001). Today, more than 70% of the mountainous areas are marred with nearby infrastructure (< 5 km), while more than 90% of them were virtually undisturbed in the early 20th century (Nellemann et al., 2003a). Norwegian mountains have thus been increasingly altered by human developments, leading to large-scale habitat loss and fragmentation in wild reindeer ranges (Vistnes et al., 2001), mainly related to renewable energy, transportation, recreation and domestic uses (Falldorf, 2013). In Norway, the population of wild reindeer is considered to have historically consisted of two to three large, free-ranging and interconnected subpopulations. Until pre-industrial times, these herds used to undertake seasonal migrations along traditional movement corridors linking their inland winter and coastal summer grazing grounds in the mountains (Skogland, 1984; Vistnes et al., 2004). Over the last 100 years of piecemeal infrastructure development, extensive habitat modifications and increased levels of human disturbance have caused the wild reindeer population to be split into 23 distinct herds, most of which have largely reduced their migrations because of infrastructure blocking important movement corridors, leaving reindeer with scarce options to migrate (Panzacchi et al., 2013b). Accordingly, like most caribou and reindeer populations worldwide, Norwegian herds are severely affected by human activities and the associated network of

infrastructures, with significant effects on distribution, population dynamics and overall demographic condition (see Vistnes et al., 2004 for a review). Indeed, habitat loss and fragmentation are currently considered the major threats to wild reindeer in Norway (Falldorf, 2013; Kjørstad et al., 2017; Nellemann et al., 2003a).

Besides being a species of high ecological, social and economic value, reindeer is also a challenging concern of conservation and management relevance in Norway, since the country hosts the last remaining populations of wild mountain reindeer in Europe (Bernes et al., 2015; Kaltenborn et al., 2014; Skogland, 1986). This situation has led to the recognition of wild reindeer vulnerability and entrusted Norway with an international responsibility for sustainably managing its population of wild mountain reindeer (Kofinas et al., 2000; Vistnes & Nellemann, 2008). To grant the future of this flagship species in Europe, Norway has committed to strive for 'maintaining viable population units within ecologically functioning and suitable habitats for the future' (Kjørstad et al., 2017). A concrete response recently provided by the Norwegian government with respect to this commitment involves the implementation of an environmental quality standard meant to assess the status of the 23 wild reindeer population units in the years to come, and to identify the factors that negatively affect their habitat. The ensuing quality norm (QN) was developed by a group of wild reindeer experts appointed by the Norwegian Environmental Agency[1] (see Kjørstad et al., 2017 for details). It consists of three assessment criteria focused on population condition, lichen resource, and anthropogenic habitat loss, each being assessed on a three level ranking: good, medium, and bad, the final score of each reindeer area being set by the worst result among the three criteria. The 'population criterion' focusses on calf body mass, reproduction rate, sex ratio, genetic diversity, and diseases. The criterion on lichen pastures evaluates the density of lichen, which is an important forage resource for reindeer during winter. Lastly, the third criterion on the loss of habitat due to human disturbances both quantifies the loss of seasonal habitat (QN3A, pp. 138 in Kjørstad et al., 2017) and the loss of functional connectivity (QN3B). The habitat loss is evaluated with respect to the three main seasonal requirements of wild reindeer, namely the summer grazing, winter grazing, and calving ground. The present thesis is related to the QN framework, and particularly to the QN3A criterion, which will be further investigated in the following analyses.

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[1] The Norwegian Environment Agency is a government agency under the Ministry of Climate and Environment (https://www.environmentagency.no/norwegian-environment-agency/about-us/).

OBJECTIVES

Understanding and quantifying anthropogenic habitat loss (i.e., the loss of seasonal habitat due to human disturbances) in wild reindeer ranges represents a critical step in determining whether these areas will be able to support sustainable population units in the future. Furthermore, this is a paramount requirement for achieving effective land-use management that would ensure the preservation of wild reindeer habitat and the long-term persistence of its populations in Norway, and more broadly in Europe. Rooted in this framework and driven by the ambition to contribute to it, the current thesis was conducted with the following core research question to address: what is the impact of human disturbances on wild reindeer summer ranges in southern Norway? More specifically, it aims at:

Obj. 1- Quantifying the amount of anthropogenic habitat loss and characterizing the distribution of the human footprint in wild reindeer summer ranges.

Obj. 2- Evaluating habitat quality in wild reindeer summer ranges and identifying its main limiting factors.

Obj. 3- Measuring the impact of major anthropogenic activity sectors in wild reindeer summer ranges and identify the main single drivers of anthropogenic habitat loss.

Furthermore, the purpose of this thesis, based upon existing habitat selection models, aims at synthesis of modeling outputs and focuses on exploring, interpreting and communicating these results. The RSFs used in this research are powerful tools that provide a very helpful, but highly formalized, framework for quantifying the impact of human disturbances on landscape and species habitat. Besides the fundamental scientific goals it pursues, the current thesis thus also aims to make its outcomes pragmatic and accessible for practitioners, stakeholders and decision-makers, with a view to inform management strategies and policies. Consequently, this research is intended to be of public relevance and will hopefully find uses in applied conservation.

MATERIAL AND METHODS

1. <u>Study area</u>

The geographic scope of this assessment was defined based on the current distribution of wild mountain reindeer (*Rangifer tarandus tarandus*) in Norway. The Norwegian wild reindeer population currently consists of 25,000 to 30,000 reindeer distributed in the mountainous areas of southern Norway, from Sør-Trøndelag and further southward (5–12°E, 58–63°N). These are divided in 23 herds, the largest of which, Hardangervidda, counts ca.10 000 individuals (https://www.villrein.no/) (Fig. 2a). The study area encompasses the 23 official areas dedicated for wild reindeer management in Norway (Fig 2b). These areas are mostly located above the tree line, in alpine environments and are influenced by strong east–west climatic and topographic gradients. Wild reindeer habitat is thus composed of relatively mild, high-precipitation, coastal areas in the west, where the oceanic climatic influence is associated with rugged terrains and high elevation fjord relief, while colder, lower-precipitation inland areas experiencing a continental climate are found in the east, with a smoother terrain relief of mountain plateau (Bakkestuen et al., 2008). These 23 areas are largely bounded by transportation infrastructure, which impedes wild reindeer movements and encloses population units (Panzacchi et al., 2013a).

(a)

(b)

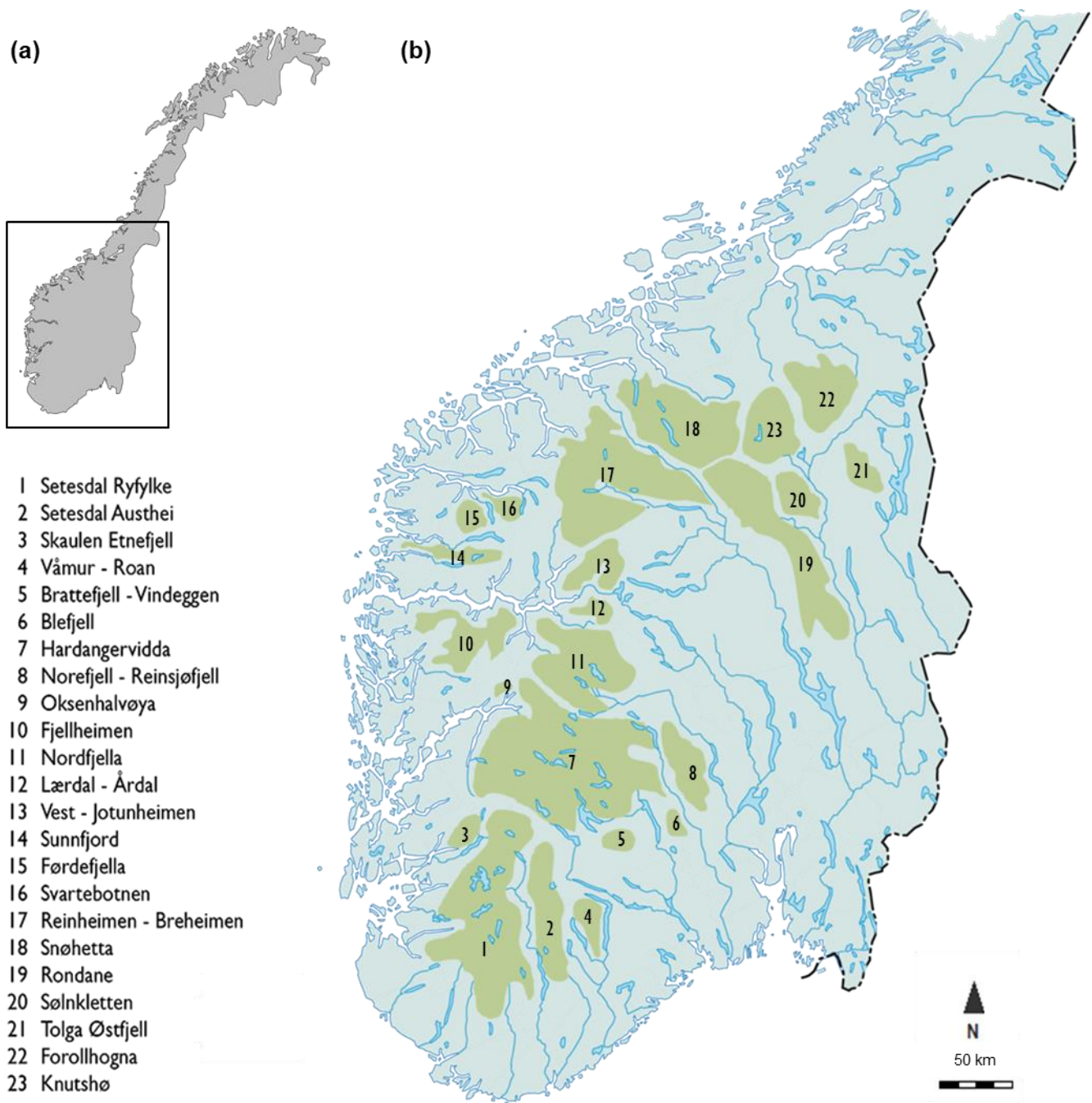|	
1	Setesdal Ryfylke
2	Setesdal Austhei
3	Skaulen Etnefjell
4	Våmur - Roan
5	Brattefjell -Vindeggen
6	Blefjell
7	Hardangervidda
8	Norefjell - Reinsjøfjell
9	Oksenhalvøya
10	Fjellheimen
11	Nordfjella
12	Lærdal - Årdal
13	Vest - Jotunheimen
14	Sunnfjord
15	Førdefjella
16	Svartebotnen
17	Reinheimen - Breheimen
18	Snøhetta
19	Rondane
20	Sølnkletten
21	Tolga Østfjell
22	Forollhogna
23	Knutshø

Figure 2

(a) Location of the study area in Norway and (b) detailed view of the 23 wild reindeer management areas that comprise the study area – which corresponds to the distribution range of wild mountain reindeer in southern Norway and coincides with its European distribution range too (modified from https://www.villrein.no).

2. <u>Habitat selection models and reindeer GPS data</u>

To investigate the issue of anthropogenic habitat loss in wild mountain reindeer summer ranges, the individual and cumulative effects of human disturbances were quantified through habitat selection modeling. Wild reindeer space use patterns were studied in relation to the human footprint in a 'use versus availability' design, where used locations were statistically compared to available ones in environmental space. Here, habitat selection was modeled at the local scale based on reindeer location data for the summer season and remote sensing GIS information on natural and anthropogenic habitat covariates (see environmental layers in the next section). GPS data from 257 radio-collared adult females from 10 of the largest herds on their summer range were used to describe wild reindeer habitat use. The July 1st – August 15th time period was taken as representative of the summer season to avoid including data from the end of the spring migration or from the beginning of the autumn migration, as well as to evaluate habitat selection outside the hunting season (August 20th – September 10th).

As a methodological basis for the current assessment, anthropogenic habitat loss was investigated using wild reindeer-specific RSFs, adapted from Panzacchi et al. (2015, in prep.). RSF models yield outputs that are proportional to the probability of use of a resource unit, while assuming unrestricted access to all of them (Boyce et al., 2002). Although resource units can be approached in many different ways, a common definition, that is the one chosen here, treats resource units as fixed-size geographic areas, here set as pixels of 100 x 100 m resolution from GIS. Consideration of scale is fundamental in disturbance studies since habitat selection occurs at multiple spatial levels to address species biological requirements (Johnson, 1980). The home range constitutes a hosting entity where all individuals of a same population unit are subjected to similar seasonal habitat conditions and anthropogenic influences. It is fairly well documented that wild reindeer habitat use tends to vary in space according to habitat conditions found at the regional and the local scales. Accordingly, the home range is a level of good relevance for habitat selection studies in reindeer, where regional-scale analyses are advised (Vistnes & Nellemann, 2008). For that reason, Panzacchi et al. (2015, in prep.) analyzed simultaneously data from all monitored herds to allow inferences across the 23 populations, but matched used locations with those available within a population's range to account for local differences in available habitat. Subsequent analyses were mostly focused on management areas described above, which approximate home ranges of the 23 herds, thus leading to a regional-scale, herd-level assessment of anthropogenic habitat loss.

3. <u>Environmental layers</u>

Norwegian wild mountain reindeer inhabit large areas that face the impact of anthropogenic landscape changes as an overlay to the natural disturbance regime of alpine ecosystems that governs spatiotemporal distribution and availability of landscape features, food resource, and thus habitat. Twenty-five habitat covariates found to be meaningful for predicting and modeling habitat selection in wild reindeer were used in the current study (Tab. 1). Habitat selection models were provided with a total of 25 environmental GIS layers accounting for human infrastructure and other anthropogenic sources of disturbance, as well as for natural resources reindeer are known to respond to, namely climate, topography, plant phenology and trophic resource (see Panzacchi et al., 2015 for further details).

Anthropogenic covariates included roads, houses, power lines, railways, grazing animals, hiking trails and tourist cottages, based on national infrastructure layers and used as proxies of the human footprint. Roads are likely avoided because of traffic rather than being perceived as threats in themselves. Traffic volume on roads is therefore a meaningful parameter influencing avoidance response in wild reindeer (Trombulak & Frissell, 2000; Wolfe et al., 2000). For that reason, summer roads were identified, in order to account for seasonal traffic restrictions, and these were categorized into low traffic and high traffic summer roads, each category operating with its own effect size and zone of influence. Houses were hypothesized to have cumulative effects according to their density, which is assumed to condition wild reindeer avoidance response. Therefore, houses were quantified using a kernel density estimation fitted with a Bartlett ('tent') distribution and a 10 km radius. The power line variable only accounts for power lines without nearby roads or railways. This distinction was made because the effect of power lines is significantly different whether these are close to roads or railways (Reimers et al., 2007). The effect of the power lines located next to such infrastructures is for its part already comprised in the related layers, since there are virtually no roads or railways without power lines next to them. Main hiking trails were identified based on their frequency of use inferred from the Trail Use Index (TUI, Gundersen et al., 2019) that measures tourist volume (hikers per day and per km trail). Three types of tourist cottages were distinguished, each quantified using kernel density estimations, as for houses. A first distinction was made between private and public cabins, which differ in number, intensity of use and location with respect to wild reindeer habitat. As a rule, private cabins tend to be more numerous than public cabins, while being less intensively frequented, and located more on the edge

of wild reindeer habitat. Then, public cabins were categorized based on their intensity of use during the summer season, making a distinction between low summer use and high summer use public cabins. Finally, grazing animals (beitedyr) from domestic livestock were taken as an additional variable. While not being an infrastructure as such, this land use may represent a source of disturbance for reindeer. Although industrial activities, namely related to energy production, are quite important in Norway, data on mines, wind parks and other industrial infrastructures were left out of the current assessment. Indeed, these fell outside the study area since being either absent from wild reindeer ranges, or too few for robust estimation. Except for hydropower reservoirs, industrial infrastructure is mostly a concern for semi-domestic reindeer (see e.g., Bergamo, 2011; Flydal et al., 2004). Conversely, these reservoirs are the major source of anthropogenic land-cover changes in wild reindeer ranges. However, they represent a challenging type of infrastructure to treat in disturbance studies, as a proper assessment of their effect requires knowledge of the pre-reservoir water levels. These data are hard to come by, as most reservoirs pre-date commonly available satellite imagery. Virtually, all reservoirs are established in areas that contained significant amounts of natural lakes, hence assuming that all area now covered by reservoirs previously corresponded to reindeer habitat would result in a significant overestimation of the human footprint. Instead, the opposite assumption was made, thus the current assessment will be a fairer underestimation of the human footprint. Results were interpreted keeping this simplification in mind for the discussion where this methodological choice is further developed.

Climate, topography, plant phenology and trophic resources also play a significant influence in wild reindeer habitat selection. These variables were therefore used as proxies of natural suitability. Forage availability was approached using the NORUT vegetation map (Johansen, 2009, resolution 100 m), reclassified into forest, lichen, lichen forest, bogs, grasses, heather ridges, heather lowland, meadows, rocks and ice, snow bed, and other land covers. Because plant phenology, and thus forage accessibility, is closely related to snow accumulation, climatic conditions were assessed through solar radiation, as a proxy of sun exposure favoring snow melt, and snow days, as a proxy of winter length and the onset of spring. Plant phenology was quantified using the day of onset of spring from the Normalized Difference Vegetation Index (NDVI, Beck et al., 2006). Terrain relief was quantified using the Topographic Position Index (TPI, radius 2500 m), which measures the relative topography by comparing points elevation to the mean elevation of a determined neighborhood. Information on slope and lakes was also included in the natural suitability.

4. <u>Model formulation</u>

The present research uses predicted RSF values as input for further analysis. These RSFs were fitted with logistic regression, using on a log link function, to model habitat selection in wild reindeer according to a set of habitat covariates. The selection function is then given by the logistic discriminant of the regression:

$$w(x) = \exp(\beta_1 \times x_1 + \beta_2 \times x_2 + \cdots + \beta_n \times x_n) \tag{1}$$

where $w(x)$ represents the selection ratio, which expresses the relative probability that reindeer selects a given resource unit represented by a suite of habitat covariates $x_1 + x_2 + \ldots + x_n$. In RSFs, each habitat covariate is associated with a variable- and species-specific selection coefficient (β_i), also referred to as the effect size. This parameter translates the strength of influence the corresponding variable has on habitat selection in the species. In the latter equation (Eq. 1), β_i stands for the effect size of the ith habitat variable. In addition, for the kernel density computation of the anthropogenic variables, a buffer radius or a zone of influence (ZOI) was selected, which represents the area of reduced occupancy that results from avoidance in the vicinity of human developments. By including a ZOI in habitat selection functions, the effect size is adjusted according to the distance from the disturbance source. Thus, the subsequent avoidance response – modeled through the RSF – declines linearly as a function of distance, within a certain radius from the disturbance source given by the ZOI, before falling down to zero once this limit is exceeded. While selection function coefficients were obtained through model fitting (maximum likelihood), the best ZOI for each variable was found through iterative model selection based on minimizing AIC. The selection coefficients (β_i) and zones of influence (ZOI$_i$) corresponding to each habitat variable included in the current assessment are provided in Table 1. Finally, in its simplest, the selection function models a linear response to the habitat variable under consideration. Although most habitat variables were indeed expected to induce a linear response, some others were hypothesized to be selected with an optimum value and an associated breadth along the resource gradient (Gaussian profile). These variables, namely snow days, TPI and slope, were consequently modeled through second degree polynomials, i.e. including squared terms in addition to the linear ones, which corresponds to a Gaussian shaped response curves on the linear scale.

Table 1

Names and descriptions of habitat covariates used to model habitat selection of wild mountain reindeer on summer ranges in southern Norway, associated index (i), selection coefficients (β_i), zones of influence (ZOI_i) and standard errors ($se(\beta_i)$).

i	NAME	DESCRIPTION	β_i	ZOI_i (m)	$se(\beta_i)$
ANTHROPOGENIC COVARIATES					
1	roads_summer_high_1000	High traffic summer roads	-1.94E+01	1000	1.19E+00
2	roads_summer_low_5000	Low traffic summer roads (forest and private roads)	-2.48E+01	5000	4.24E-01
3	powerlines_noroadtrail_1000	Power lines without nearby roads or railways	-4.78E+00	1000	5.11E-01
4	railway_100	Railways	-1.10E+01	100	2.11E+02
5	houses_10000	Houses	-1.18E+02	10000	2.76E+00
6	trails_log_pseudotui_2500	Hiking trails	-7.83E-02	2500	2.21E-03
7	private_cabins_1000	Private cabins	-1.82E+01	1000	8.92E-01
8	pub_cabins_summer_high_10000	Public cabins of high use during summer	-4.16E+03	10000	2.18E+02
9	pub_cabins_summer_low_1000	Public cabins of low use during summer	-6.36E+01	1000	1.24E+01
10	beitedyr_5000	Grazing animals from domestic livestock	-2.93E-02	5000	5.89E-04
NATURAL COVARIATES					
11	dem_tpi_2500_50m	Topographic Position Index (TPI), linear term	-4.13E-03	2500	8.19E-05
11'	l(dem_tpi_2500_50m^2)	Topographic Position Index (TPI), squared term	-9.60E-06	2500	3.91E-07
12	slope	Slope, linear term	5.69E-02	NA	1.72E-03
12'	l(slope^2)	Slope, squared term	-1.77E-03	NA	4.93E-05
13	snow_days_500	Snow days, linear term	1.36E-01	NA	2.93E-03
13'	l(snow_days_500^2)	Snow days, squared term	-2.59E-04	NA	6.33E-06
14	solar_radiation_10m_july	Solar radiation	-2.63E-05	NA	1.48E-06
15	grasses	Grasses	6.24E-01	NA	2.01E-02
16	heather_lowland	Heather lowland	3.60E-01	NA	1.99E-02
17	heather_ridges	Heather ridges	-8.93E-02	NA	1.98E-02
18	skog	Forest	4.23E-01	NA	2.16E-02
19	lavskog	Lichen forest	5.05E-01	NA	4.10E-02
20	lichen	Lichen	-1.31E-01	NA	3.77E-02
21	meadows	Meadows	1.80E-01	NA	3.33E-02
22	myr	Bogs	1.81E-01	NA	2.74E-02
23	snowbed	Snow bed	5.77E-01	NA	1.72E-02
24	norut_impediment_100_100m	Rocks and ice	-8.18E-01	NA	2.17E-02
25	noclass	No vegetation land cover	-7.34E-01	NA	6.08E-02
26	dyrka	Other land covers	-4.85E-01	NA	5.85E-01
27	lake_nores	Lakes that are not reservoirs	-2.47E+00	NA	7.74E-02
28	reservoir	Hydropower reservoirs	-3.23E+00	NA	2.03E-01

MATERIAL AND METHODS

5. <u>Measuring the human footprint</u>

Predictive modeling of habitat selection provides a powerful framework for quantifying the impact of human disturbances on landscape and species habitat, with broad applicability in cumulative impacts assessment and human footprint mapping. Here, the outputs of RSFs were used to assess anthropogenic habitat loss in wild reindeer summer ranges. Anthropogenic habitat loss was investigated in close relation to the concept of habitat quality. Habitat quality can be seen as an integrated measure of the natural suitability of the habitat and the human footprint that is 'stamped' upon it. The current assessment was based on the assumption that uneven habitat use, resulting from selection and avoidance processes, correlates with habitat quality. Accordingly, the approach proposed in this thesis relies on using the relative probability of use provided by selection functions as a proxy of habitat quality. While, the impact of anthropogenic covariates, hereafter referred to as the human footprint, was evaluated through the loss of habitat quality induced by these disturbances, which was measured by means of changes in the relative probability of selection.

Depending on the set of covariates included in the selection function, three main habitat components were defined in the current framework. When the RSF was generated with only natural covariates (Eq. 2), the outputs were interpreted as the natural suitability (η) of the habitat. This first component therefore reflects the natural quality of the habitat. It was used to determine the ecological value of the habitat for the species and subsequently model wild reindeer potential habitat in the absence of human developments. Then, the same reasoning was followed with anthropogenic covariates only, to approximate the potential human footprint (Λ). As the RSF models selection, an additional complement-to-unity transformation was operated to translate the results of selection in terms of avoidance (Eq. 3). This transformation allows for a more intuitive and straightforward interpretation of the inherent footprint index, which is a composite measure accounting for the cumulative impact of all human disturbances on the landscape. Finally, the realized suitability (τ) was estimated by including both natural and anthropogenic covariates in the model (Eq. 4). This component measures the cumulative effect of natural and anthropogenic drivers on the habitat. Hence, it reflects the actual remaining suitability of the habitat once the effect of anthropogenic disturbances on the habitat has been subtracted from its natural suitability, and it was therefore interpreted as the habitat quality.

$$\eta = \exp(\beta_{11} \times x_{11} + \cdots + \beta_{28} \times x_{28}) \qquad (2)$$

$$\Lambda = 1 - \exp(\beta_1 \times x_1 + \cdots + \beta_{10} \times x_{10}) \qquad (3)$$

$$\tau = \exp(\beta_1 \times x_1 + \cdots + \beta_{28} \times x_{28}) \qquad (4)$$

The definition of the human footprint is central to the current methodology since habitat loss was assessed through it. To quantify the amount of habitat affected by avoidance, i.e. the amount of anthropogenic habitat loss, a key distinction was drawn between the potential human footprint (Λ), defined here above (Eq. 3), and the realized human footprint (ϕ). The potential footprint is a theoretical metric based on the integration of the effect size and the ZOI. It can therefore be considered as the volume of habitat subjected to disturbance, regardless of the underlying natural adequacy of this habitat for the species given its ecological preferences and requirements. However, areas of high natural suitability are more biologically significant for the species, and thus more damaging to lose than less naturally suitable ones. In other words, habitat loss was considered to occur at the overlap between the species ecological niche, described by the natural suitability, and the potential human footprint. Hence, the current assessment paid particular attention to the natural suitability of the habitat encompassed in the disturbance volume described by the potential footprint, in order to evaluate habitat loss from the species perspective. Accordingly, the realized human footprint (ϕ) was defined as the potential footprint of a resource unit (Λ) weighted by its natural suitability (η), thus reflecting the loss of suitable habitat (Eq. 5). This metric was used to quantify anthropogenic habitat loss:

$$\phi = \eta \times \Lambda \qquad (5)$$

6. <u>Analyses</u>

Data processing and analyses were performed in R version 4.0.0 (2020). Because the exponential $\exp(\beta \times x)$ is not bounded to 1, RSFs yield values that are proportional, but not necessarily equal, to the probability of use. It is therefore common practice to rescale RSF modeling outputs that are not naturally ranging from 0 to 1 by means of multiplication or addition of a constant value, hereafter called the rescaling cap. The current outputs accounting for the realized suitability and the natural suitability components were rescaled before analysis, using a rescaling cap arbitrarily set at the 75th quantile of the natural suitability. By definition, the potential human footprint scaled

between 0 and 1, as in the absence of human infrastructures no effect can be detected. Subsequent rescaled values were all ranging from 0 to 1 and could therefore be interpreted as the probability of use. The relevance of this transformation, as well as its implications for subsequent analyses, are discussed further in this thesis. However, it should be noted that the somewhat arbitrary choice of this rescaling cap directly affects the results from the following analyses, as the rescaling cap determines the total amount of wild reindeer habitat that is considered ideal from a biophysical perspective ($\eta = 1$). Thus, with the current rescaling cap, 25% of this habitat was considered ideal, which seemed a reasonable albeit somewhat arbitrary.

6.1. <u>Percentage of habitat loss</u>

The cumulative impact of all human disturbances on wild reindeer summer ranges was first assessed by quantifying the total amount of anthropogenic habitat loss in each management area. The first analysis evaluated the proportion of seasonal habitat lost due to the human footprint. This analysis was conducted in reference to the environmental quality norm framework described in the introduction, and was inspired by the expert-based methodology developed for the assessment of the criterion QN3A on the loss of seasonal habitat (Kjørstad et al., 2017). Such expert-based approaches are often the only available option for such assessments in the absence of other data. This methodology uses focal areas, which are smaller areas within wild reindeer management areas where there is a suspicion for a significant human impact limiting habitat quality, as a measurement unit. Hence, the expert-based assessment assumes the effect of human disturbances is negligible outside of focal areas. Habitat loss is assessed by experts within each focal area, using a two-step approach. The percentage of use reduction during the past 10 years, compared to the previous 50 years, is first assessed in each focal area. Then, all focal areas within a same management area are integrated to compute the amount of seasonal habitat subjected to medium (50 – 90%) and high (> 90%) use reduction. This amount of reduced-use seasonal habitat is subsequently compared to the total amount of seasonal habitat available in the management area, in order to compute a proportion of habitat loss and evaluate whether a small (<10%), medium (10-20%) or large (>20%) amount of the seasonal habitat is lost due to human disturbances. The management area finally gets a seasonal score based on the percentage of seasonal habitat affected by medium and high use reduction, following a traffic-light system: green (good), yellow (medium), and red (bad).

However, because habitat selection modeling constitutes a powerful tool for assessing the impact of human disturbances on species habitat, the current study embraced the opportunity lying in the models developed by Panzacchi et al. (2015) to address the issue of data limitation and implement a model-based approach for the assessment of seasonal habitat loss in wild reindeer ranges. The alternative that is proposed here integrates the two steps of the expert-based approach into a single step by computing a continuous metric reflecting the percentage of anthropogenic habitat loss. The model-based approach directly depends on RSF outputs corresponding to the realized human footprint (ϕ) and the natural suitability (η); both components can be interpreted as measures of land area. Since the resource unit is defined as a pixel of resolution 100 x 100 m in the current framework, each pixel therefore represents a land area of 0.01 km². Accordingly, the natural suitability, which ranges from 0 to 1 and scores to the natural adequacy of the habitat for the species, can actually be interpreted as the amount of ideal habitat that is comprised in the pixel. For instance, if a pixel has a natural suitability of 0.32, it also means this pixel is made at 32% of ideal habitat, or that it contains 0.32 x 0.01 = 0.0032 km² of ideal habitat available for reindeer. Following the same reasoning, the realized human footprint provides an approximation of the amount of ideal habitat that is lost due to human disturbances in the pixel. Hence, integrating these two metrics at the level of the management area provides an estimation of the amounts of seasonal habitat that are available, on the one hand, and lost due to human disturbances, on the other hand. To compute the corresponding percentage of habitat loss (π), the realized human footprint (ϕ) and the natural suitability (η) of all the pixels comprised in the assessed management area were summed, and the ratio of these two sums was interpreted as the proportion of naturally ideal habitat lost due to avoidance of human disturbances (Eq. 6):

$$\pi = \frac{\Sigma \phi}{\Sigma \eta} \times 100 \tag{6}$$

6.2. Habitat quality and its main limiting factors

The second analysis makes a first step in the identification of landscape features that negatively affect living conditions in wild reindeer ranges. Here, the human footprint was evaluated as a limiting factor of habitat quality, along with natural unsuitability. Habitat quality and its main limiting factors were investigated locally, in a 'natural vs anthropogenic' design, through a ternary analysis using the *Tricolore* function in the R package *tricolore* (*v1.2.2.*; Schöley, J. and

Kashnitsky, I.; 2020). This analysis was based on three-dimension, compositional data provided by the following components: the natural unsuitability ($1 - \eta$ or $1 - \phi - \tau$), the realized human footprint (ϕ) and the realized suitability (τ), together summing to one. These components respectively account for the limiting effect of natural causes on habitat quality, the limiting effect of cumulative anthropogenic causes on habitat quality, and the habitat quality itself. Each pixel was then color-coded by the *Tricolore* function, according to its three-part composition reflecting the importance of each habitat component in the pixel. Color-coded compositions were used to generate a continuous raster map representing habitat quality and its main limiting factors in each pixel of the study area. Summaries were compiled for each of the 23 management areas, where the three components were valued as their integrated average among all pixels in the assessed management area, and expressed as percentages for pie charts. The geographical distribution of the human footprint and the natural unsuitability provide the background to interpreting the π values yielded by the previous analysis.

6.3. Sectoral analysis of the human footprint

The third and fourth analyses took the question of the limiting factors a step further and identify the main sources, or drivers, of anthropogenic habitat loss. This question was first explored using a sectoral approach, where anthropogenic habitat variables were grouped into three sectoral categories, namely the domestic sector, the recreational sector and the agricultural sector. The domestic sector encompasses houses, power lines, railways, as well as high and low traffic summer roads. The recreational sector includes all infrastructures related to recreational uses of the mountains and tourism, i.e. hiking trails, private cabins and public cabins of high and low use during summer. Domestic livestock (beitedyr) represented the agricultural sector. The realized human footprint was decomposed along the sectoral dimension and investigated locally through a ternary analysis using the *Tricolore* function in the R package *tricolore* (*v1.2.2.*; Schöley, J. and Kashnitsky, I.; 2020). This analysis was based on three-dimension, compositional data provided by the following components: the domestic footprint (ϕ_{dom}, Eq. 7), the recreational footprint (ϕ_{recre}, Eq. 8), and the agricultural footprint (ϕ_{agri}, Eq. 9), together summing to one. These components respectively account for the sectoral realized human footprint of domestic uses, the sectoral realized human footprint of recreation and tourism, and the sectoral realized human footprint of agriculture. Each pixel was then color-coded by the *Tricolore* function, according to its three-part composition

reflecting the importance of each sector in the cumulative realized human footprint of the pixel. Color-coded compositions were used to generate a continuous raster map representing the relative importance of each of the three sectors of human activity in the pixel. In addition, each pixel was assigned an opacity level that is either zero when the cumulative realized human footprint of the pixel is low ($\phi < 0.5$), or directly proportional to the cumulative realized human footprint of the pixel otherwise ($\phi \geq 0.5$). Summaries were compiled for each of the 23 management areas, where the three sectoral footprints were valued as their integrated average among all pixels in the assessed management area, and expressed as percentages in the form of pie charts.

$$\phi_{dom} = \eta \times \Lambda_{1\text{-}5} = \exp(\beta_{11} \times x_{11} + \cdots + \beta_{28} \times x_{28}) \times (1 - \exp(\beta_1 \times x_1 + \cdots + \beta_5 \times x_5)) \tag{7}$$

$$\phi_{recre} = \eta \times \Lambda_{6\text{-}9} = \exp(\beta_{11} \times x_{11} + \cdots + \beta_{28} \times x_{28}) \times (1 - \exp(\beta_6 \times x_6 + \cdots + \beta_9 \times x_9)) \tag{8}$$

$$\phi_{agri} = \eta \times \Lambda_{10} = \exp(\beta_{11} \times x_{11} + \cdots + \beta_{28} \times x_{28}) \times (1 - \exp(\beta_{10} \times x_{10})) \tag{9}$$

6.4. Single-driver analysis of the human footprint

To further refine the sectoral approach and test the significance of each anthropogenic variable as a single driver of habitat loss, the human footprint was further decomposed among all anthropogenic variables. The fourth analysis was conducted with the purpose to take a detailed view on the diversity of anthropogenic disturbances within the study area and identify the main drivers of habitat loss. The human footprint was fully decomposed and the single impact of the ith disturbance variable was assessed through its individual realized human footprint (ϕ_i, Eq. 10), computed as follows:

$$\phi_i = \eta \times \Lambda_i = \exp(\beta_{11} \times x_{11} + \cdots + \beta_{28} \times x_{28}) \times (1 - \exp(\beta_i \times x_i)) \tag{10}$$

Individual footprints were computed for each single driver at the regional scale, in each management area, as their integrated average among all pixels in the assessed management area. To allow for footprints comparison between drivers, as well as between areas, these average values were rescaled using their maximum value, here found to be the footprint of houses in Oksenhalvøya. Area-specific radar charts were computed and stacked into a composite radar chart. In their detailed form (area-specific), radar charts allow the identification of the main, area-specific drivers of anthropogenic habitat loss, while the composite radar chart summarizes this information for the whole wild reindeer distribution in Norway.
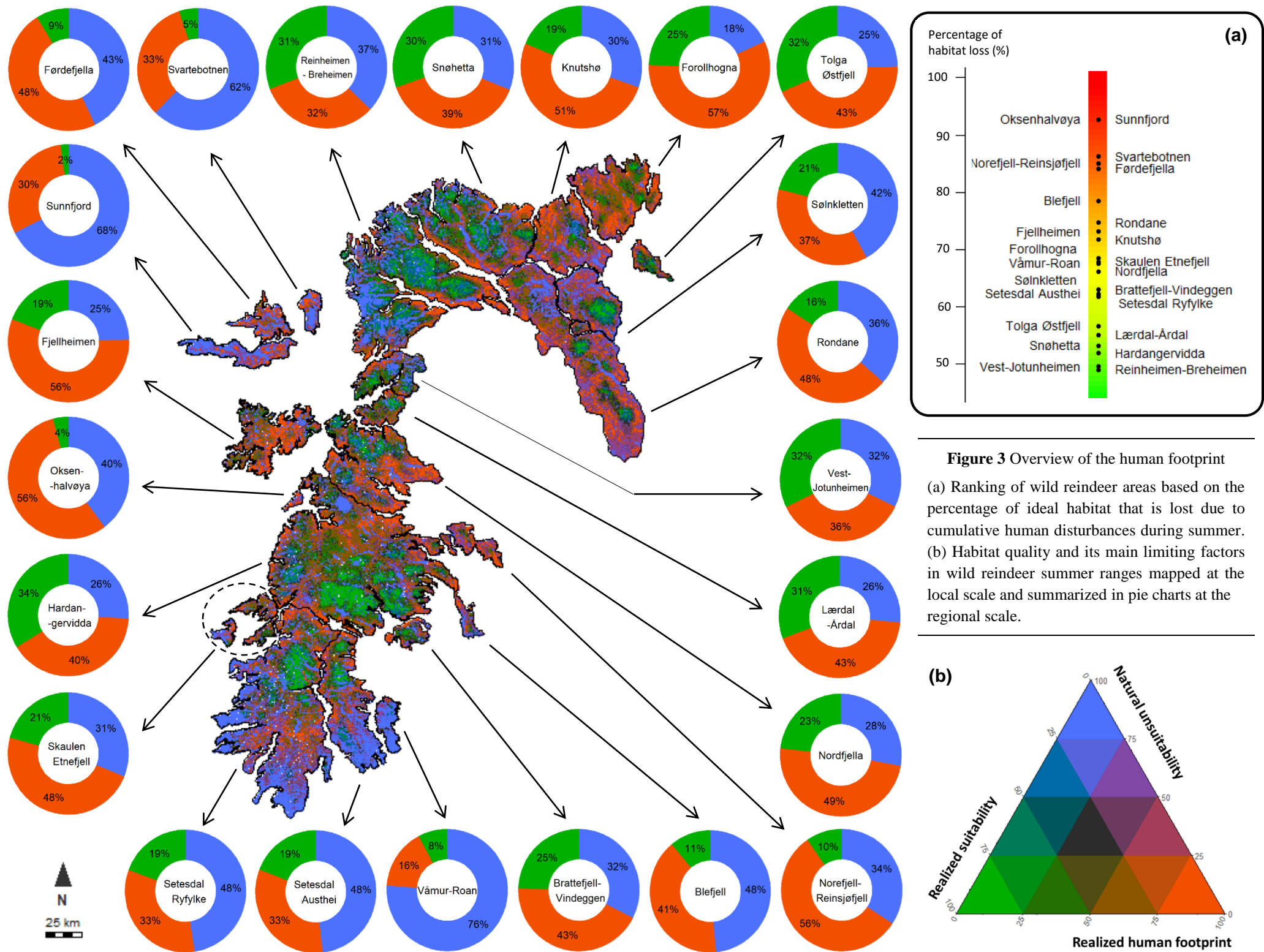
RESULTS

1. Percentage of habitat loss

Avoidance of human disturbances was found to result in substantial cumulative habitat loss for wild reindeer on summer range throughout the whole study area. The proportion of ideal seasonal habitat lost due to human disturbances, measured by the percentage of habitat loss (π), was larger than 50% in virtually all of the 23 management areas (Fig. 3a). According to the current models, Norwegian herds have lost between 48% (in Reinheimen-Breheimen) and 93% (in Sunnfjord and Oksenhalvøya) of their ideal habitat on summer range due to human activity and infrastructure. Population units were unevenly affected by anthropogenic habitat loss depending on their spatial distribution. In total, 12 of the 23 herds have experienced habitat loss equivalent to 60-80% of their ideal summer habitat. While 6 other herds lost less than 60% of ideal habitat, the 5 remaining ones were more heavily impacted, with a percentage of habitat loss greater than 80%. Accordingly, management areas could be ranked based on their percentage of cumulative anthropogenic habitat loss, as a basis for prioritizing management.

2. Habitat quality and its main limiting factors

Wild reindeer habitat quality varied within the study area, both locally and at the regional scale, but it was always limited either by natural conditions or by anthropogenic disturbances in every management area (Fig. 3b). The continuous raster map representing habitat quality and its main limiting factors at the local scale displays unicolor pixels, the color of which is directly depending on the importance of each of the three habitat components in the pixel and is thus a composite color, mixing green (realized suitability), blue (natural unsuitability) and red (realized human footprint) in corresponding proportions. Locally, habitat quality was found to be good in a few spots, such as in north Setesdal Ryfylke or south Hardangervidda, where patches of green pixels indicate a clear dominance of the realized suitability in corresponding locations. However, reported on the regional scale, where the three components are detailed as their integrated average, none of the 23 management areas appeared to have a dominant realized suitability, compared to the two other components of this analysis, namely the natural unsuitability and the realized human footprint of cumulative disturbances. Natural unsuitability was identified as the main factor limiting habitat quality in some areas including Våmur Roan, Svartebotnen or Sunnfjord, where this component is

clearly prevailing on the realized suitability and the realized human footprint. At the local scale, a large proportion of blue pixels characterized these areas. Conversely, habitat quality was mostly limited by the human footprint in red pixels, which dominates such areas as Fjellheimen, Oksenhalvøya, Forollhogna or Norefjell-Reinsjøfjell. Besides these three extreme situations (green, blue and red) indicating a clear dominance of one of the three components (resp. the realized suitability, the natural unsuitability and the realized human footprint), many pixels displayed an intermediate color, indicating more balanced three-part compositions at the local scale. The green/red ratio in the color of each pixel represents the proportion of anthropogenic habitat loss, which is especially visible in pixels that have suitable natural conditions. Hence, locating the resulting color on the green/red axis of the color key actually provides an insight into the ratio between naturally suitable habitat that is still available (realized suitability) and naturally suitable habitat that has been lost due to human disturbances (realized human footprint). Therefore, red-tone pixels point out naturally suitable locations that were lost due to the human footprint, i.e. locations where anthropogenic habitat loss takes place.

Because π only focusses on naturally suitable habitat to assess anthropogenic habitat loss (see Eq. 6), thus somehow ignoring naturally unsuitable habitat, similar percentages of habitat loss can correspond to different habitat profiles. For instance, while Sunnfjord and Oksenhalvøya were found to have identical π values (98%), it was noted from the pie charts comparison that the realized human footprint was nearly twice more dominant in Oksenhalvøya than it was in Sunnfjord, where the natural unsuitability largely prevails instead. Beyond the sole percentage of habitat loss, the current results on how habitat quality and its limiting factors are spatially distributed within the study area (additional material in Appendix 1) is critical from a management perspective. Accordingly, the geographical distribution of the human footprint and the natural unsuitability provides a background to further interpreting the π values yielded by the previous analysis and take an overview on the human footprint in wild reindeer summer ranges, as provided in Figure 3.

Figure 3 Overview of the human footprint

(a) Ranking of wild reindeer areas based on the percentage of ideal habitat that is lost due to cumulative human disturbances during summer. (b) Habitat quality and its main limiting factors in wild reindeer summer ranges mapped at the local scale and summarized in pie charts at the regional scale.

3. <u>Sectoral drivers of habitat loss</u>

The continuous raster map representing the realized human footprint and the sectoral drivers of habitat loss provided two types of information, one related to the opacity level of the pixels, and the other to the color of the pixels. First, it was found that the realized human footprint of cumulative disturbances (ϕ) varied locally in its intensity, as evidenced by the variation in the opacity level of pixels within the study area – which was directly proportional to ϕ when larger than 0.5 (Fig. 4a). Low-footprint locations ($\phi < 0.5$) were identified, occurring in white, i.e. with a zero opacity. Such pixels occurred in south Hardangervidda or north Setesdal Ryfylke, for instance. On the contrary, pixels of substantial human footprint ($\phi \geq 0.5$) could be identified at a glance due to their high opacity level. Such pixels were present in a particularly high proportion in Forollhogna and Fjellheimen, among others. To relate on the previous analysis, management areas with a large proportion of unsuitable pixels (blue pixels) in Figure 3b now appear with a large proportion of transparent pixels (white pixels) in Figure 4a. That is because the mapped metric, namely the realized human footprint, directly depends on the natural suitability (see Eq. 5).

Then, the color of each pixel is a composite color, which directly depends on the importance of each of the three components, i.e. the three sectors of human activity, in the pixel, thus mixing pink (domestic sector), orange (agricultural sector) and turquoise (recreational sector) in corresponding proportions. Hence, besides varying in its intensity, the realized human footprint was also found to differ between reindeer areas based on its sectoral composition, both at the local and regional scales (Fig. 4a). Pie charts suggested the main sectoral drivers of anthropogenic habitat loss to vary from a management area to another. Locally, pinkish pixels were dominated by domestic uses, such as in Lærdal- Årdal, while orange tones occurred in pixels that were mostly impacted by agriculture, just like those in south Setesdal Ryfylke. A local prevalence of the recreational sector was clearly noted in Hardangervidda, where patches of turquoise pixels were found. More nuanced colors indicated a more balanced three-part composition of the cumulative realized human footprint in many pixels, with a less clear-cut dominance of the domestic, the agricultural or the recreational sector. Taking a management area-focused view on the sectoral profile of the human footprint, as provided in pie charts, the domestic sector appeared to be dominant in most cases, sometimes virtually equaled by the agricultural sector, such as in Knutshø, Skaulen Etnefjell, Fjellheimen or Reinheimen-Breheimen.

However, these results on sectoral drivers must be considered alongside the opacity level found at the local scale, i.e. the intensity of the cumulative realized human footprint, for relevant reading of the information. While the opacity level of pixels indicates most impacted locations, the color of these pixels is key to identify sectoral drivers of anthropogenic habitat loss locally. Thus, with an even greater focus on highly human-impacted areas, i.e. areas with a large proportion of opaque pixels, main impacting sectors of human activity during summer were identified. Domestic and agricultural sectors were still prevailing on the recreational sector in most cases, with a more or less sharp dominance depending on the areas. See Forollhogna, Knutshø or Fjellheimen for examples. Furthermore, the importance of the agricultural sector, in terms of human footprint on wild reindeer summer ranges, is all the more striking given the single variable (beitedyr) this sector accounts for. In contrast, Hardangervidda, which is hosting the largest herd, was shown to be clearly dominated by the impact of recreation and tourism.

4. **Single drivers of habitat loss**

Single disturbance sources displayed a wide diversity of impact within the study area, with a realized human footprint ranging from negligible to substantial depending on the drivers. (Fig. 4b). These results refined previous analysis on the sectoral drivers and showed that management areas vary in their profile of single-driver human footprint (additional material in Appendix 2), each having its own major drivers of habitat loss. Stacked together, these 23 profiles provided a composite radar chart (Fig. 4b) showing the main disturbance sources impacting Norwegian wild reindeer distribution range during summer. With regard to the domestic sector, houses and low traffic summer roads were found to have a high realized human footprint, pointing out their major significance as drivers of habitat loss for wild reindeer on summer range, as indicated by the shape and opacity of the composite polygon. The striking outcome previously made on the significance of the agricultural sector were once again noted here in the composite chart, given the large realized footprint of the beitedyr variable across the study areas. Given their substantial individual footprint within the study area, the latter disturbances were interpreted as the main drivers of seasonal habitat loss for wild reindeer in summertime. The realized footprint of hiking trails was also noted in a large proportion of management areas, but with a smaller impact on reindeer habitat. Finally, high traffic summer roads, railways, power lines and cabins were found to only have a noticeable impact on some particular areas, thus making their significance as drivers of habitat loss quite negligible at the level of the whole study area.
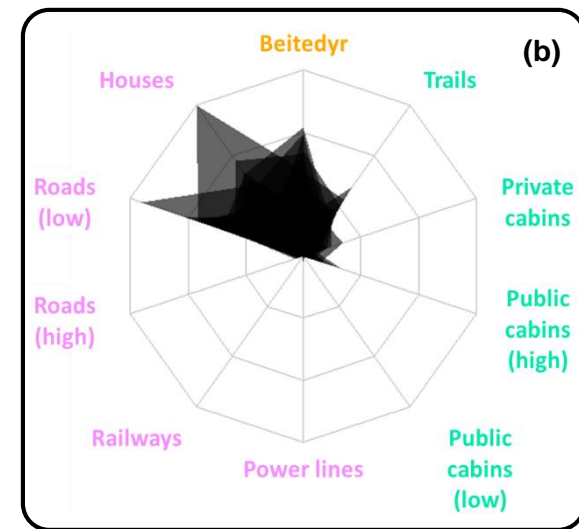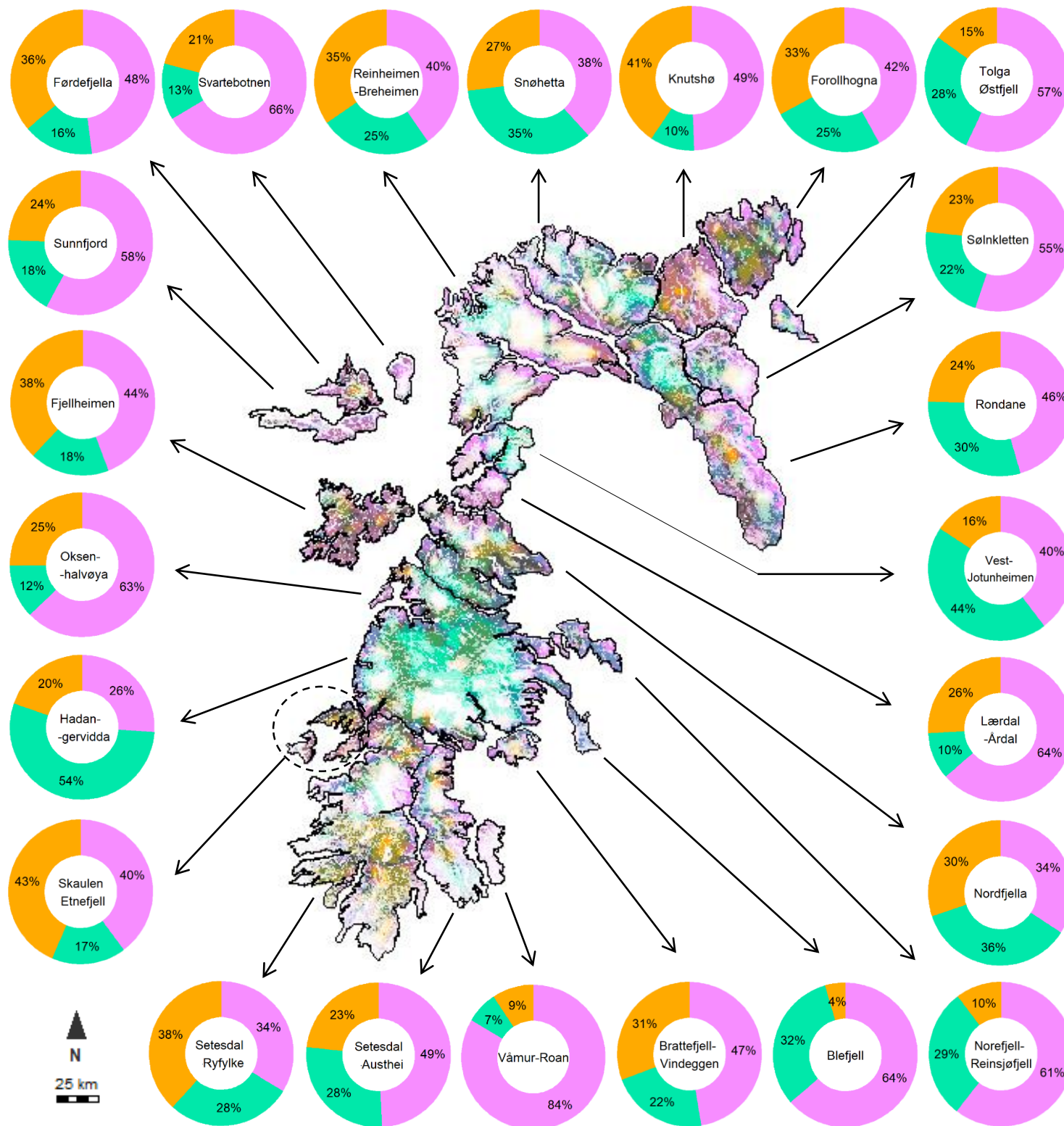
Figure 4 Detailed view of the human footprint

(a) Main sectoral drivers of anthropogenic habitat loss in wild reindeer summer ranges mapped at the local scale and summarized in pie charts at the regional scale. Each pixel has a color reflecting the contribution of each sector in its cumulative realized human footprint (ϕ) and an opacity level that is either proportional to the value of ϕ or zero when ϕ < 0.5. (b) Composite radar chart of the realized human footprint of single drivers, drawn from stacked footprint profiles of wild reindeer areas during summer and showing the main drivers of anthropogenic habitat loss in the study area.
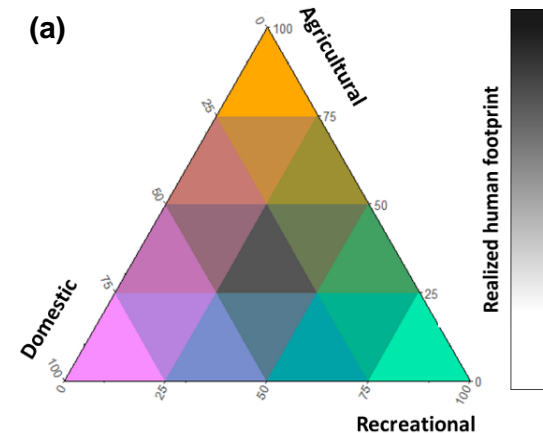
DISCUSSION

1. <u>Results discussion</u>

1.1. <u>Human footprint in wild reindeer ranges</u>

The current European distribution of wild reindeer is mostly limited to southern Norway, where it constitutes the last remaining sizable populations of this species in Europe (Kaltenborn et al., 2014). Although the Norwegian herds are closely managed and reported to be in relatively good condition against the worldwide decline of *Rangifer* populations (Solberg et al., 2017), it has been suggested that wild reindeer becomes red listed as 'near threatened' in Norway (https://www.villrein.no/). Indeed, their future in the face of increased anthropogenic development is still uncertain given their particular sensitivity to human disturbances (Benítez-López et al., 2010). That concern is all the more relevant as mountainous regions of southern Norway are among the most affected by infrastructure development and human disturbance in northern latitudes that make up the global distribution range of *Rangifer tarandus* (UNEP, 2001). The results of this study are in line with the latter concern since substantial percentages of anthropogenic habitat loss revealed by the models (ranging from 48 to 98%) corroborate the hypothesis that wild reindeer herds are already left with limited quality habitat to range during summer in southern Norway.

Alongside this general observation, some differences could be noted between the herds, primarily related to the uneven spatial distribution of the human footprint and the natural unsuitability of the habitat. Indeed, based on Figure 3, it was drawn from the comparison of Sunnfjord and Oksenhalvøya that similar percentages of habitat loss (π) could correspond to different habitat profiles. The percentage of habitat loss highlights areas where a large proportion of naturally ideal habitat is lost due to human disturbances (Figure 3a). Hence, since π only focuses on ideal habitat (see Eq. 6), it does not inform on the extent of the realized human footprint over the corresponding management area. For their part, results on the habitat quality and its main limiting factors (Figure 3b) provide a broader view and show how widespread is anthropogenic habitat loss over the management areas, as well as the extent of naturally unsuitable habitat and remaining suitable habitat that is left for reindeer. Thus, these results help to visually approximate the area covered by the realized human footprint, which somehow reflects the scope for potential action proper to each management area. Indeed, the habitat loss issue can be taken from two perspectives: the reindeer

perspective, and the manager perspective. While reindeer only cares about the realized suitability of the habitat (i.e., the remaining naturally suitable habitat that is spared from human disturbances), management is rather interested in the realized human footprint (i.e., naturally suitable habitat that is lost due to human disturbances), as being the only component we – humans – can act on to some degree, by contrast with natural unsuitability. However, in practice, the scope of action will also depend on the type of anthropogenic drivers of habitat loss that are found in each area. Indeed, one can stand that mitigation possibilities may be more limited when facing domestic uses, e.g. houses, than hiking trail, where tourist volumes could potentially be limited at certain times of the year, or grazing animals, which could be relocated towards pasture of lower conflicts with reindeer.

Furthermore, according to the current approach, habitat quality is depending on the distribution of the human footprint upon the underlying natural suitability of the habitat, the spatial configuration of both components determining human-reindeer conflict locations and habitat loss occurrence in wild reindeer seasonal ranges. Thus, realized habitat loss occurs when the human footprint is 'stamped' upon high naturally suitable habitat, the latter scoring the ecological quality of the habitat from the wild reindeer perspective. The definition of the natural suitability is therefore a crucial step in the current assessment. While RSFs provide a very powerful and formalized framework to handle habitat components such as the human footprint or the natural suitability, the rescaling of predicted values to constrain them to the [0; 1] domain, as described in the material and methods, affects subsequent analyses and results. Rescaling was here performed applying a data-driven rescaling cap to the suitability values (i.e., the 75th quantile of the natural suitability). Methodologies to get zero-to-one ranging outputs when working with RSFs should be adopted in light of existing links between habitat suitability and animal population dynamics (Matthiopoulos et al., 2015). Finding good balance between modeling efficiency and ecological consistency to link habitat suitability, as quantified by selection models, to habitat suitability from a population perspective, is not trivial and is actually a major topic for discussion (Gaillard et al., 2010). In the present study, such relationship was established through an exponential link function coupled with a rescaling cap serving as a cut-off threshold to limit highest suitability values. Just as density-dependent processes limit exponential growth in population dynamics models, the current transformation process mimics density-dependent feedback that would likely regulate pixel suitability and prevent it to grow indefinitely. Still, the rescaling method based on the setting of such rescaling cap remains quite arbitrary, without any anchorage in ecological theory. Yet, since

it determines the amount of wild reindeer habitat that is considered ideal habitat from a biophysical perspective ($\eta = 1$), the rescaling cap is central to the definition of the natural suitability. Here, the rescaling cap was arbitrarily set at the 75th quantile of the natural suitability, i.e. 25% of wild reindeer habitat is considered ideal. Upper quantiles, such as the 95th quantile set in early stages of this research, appear to be unfair and too conservative since leading much less of wild reindeer habitat (i.e., 5% with the 95th quantile) to be considered as ideally suitable. In particular, the 95th quantile led to misleading results that overestimate the amount of naturally unsuitable habitat, resulting in an unclear interpretation of the ternary analysis on habitat quality and its main limiting factors in wild reindeer management areas, what motivated the adjustment of the cap value to consider more reindeer habitat ideally suitable.

1.2.   Sectoral and single drivers of habitat loss

Recent decades have seen many consistent disturbance studies bringing compelling evidence that *Rangifer* populations, both of caribou and reindeer, are particularly sensitive to human activity and infrastructure (see Reimers & Colman, 2006; Vistnes & Nellemann, 2008; Wolfe et al., 2000 for reviews). However, few of them quantitatively compare the different types of anthropogenic disturbances wild reindeer are faced with based on their realized effect. Yet, a given disturbance source may be theoretically known to have a strong effect in the species while still being insignificant as a realized driver of habitat loss in a population given its scarcity in the landscape. Thus, for instance, roads of high use during summer were found to be of a limited impact in the current study area, while being reported as highly impacting features in disturbance literature. A possible underlying element of this result is that a significant share of Norwegian wild reindeer habitat is located in National Parks. Hence, industry and other heavy uses of the land are very restricted under these protected areas. This includes a limited amount of high traffic roads. Notwithstanding, such reindeer habitat is not free of human disturbances. Softer uses of the land, that comprise grazing animals and tourism (e.g., hiking trails), are allowed under such protected areas, involving these can occur within the boundaries of National Parks and sometimes result in significant levels of disturbance for reindeer (Gundersen et al., 2019). Besides, it was noted from the sectoral analysis of the human footprint (Figure 4a) that domestic uses were of a considerable impact in wild reindeer summer ranges.

Results on the sectoral human footprint suggested the main drivers of habitat loss to vary from one wild reindeer area to another, thus highlighting the need for targeted management of herd-specific disturbance sources. Single drivers displayed a wide diversity of impact within the study area, with a realized human footprint that could range from negligible to substantial, depending on the drivers. In particular, results on the high significance of domestic livestock (beitedyr) as a driver of habitat loss in wild reindeer summer ranges, both revealed at the sectoral and single-driver levels of analysis, draw special attention. Surprisingly, very few cumulative disturbance studies or reviews in wild reindeer report, or even consider, domestic livestock as a disturbance source. Yet, agricultural livestock are one of the most widespread types of anthropogenic land use, and although research on interference between wild free-ranging ungulates and domestic livestock is scarce, some targeted literature evidences the effects of grazing animals on reindeer (Colman, 2000; Colman et al., 2017) and other members of the deer family (Clegg, 1994; Wallace & Krausman, 1987). Interspecific interactions among sympatric ungulates are mainly reported in the form of influenced local densities and space use in wild ungulates facing livestock during summer grazing events. In Norway, domestic sheep are prevalent on alpine summer ranges, and therefore present a significant potential for disturbance during this season. Accordingly, latter results on the response of wild reindeer to grazing practices raised in this thesis should be further investigated to be confirmed and, if so, to be given greater consideration in disturbance studies.

1.3.   Further results

The present approach was developed and intended for seasonal assessment of anthropogenic habitat loss in wild reindeer ranges. Here, analyses were performed for summer as a first instance to implement the approach, following data availability. However, it is well established that reindeer and caribou sensitivity and avoidance of human developments can vary with seasons. Especially, disturbance literature reports large inter-annual variations in the ZOIs, thus suggesting clear seasonality in reindeer and caribou avoidance of human developments (Plante et al., 2018; Polfus et al., 2011). In southern Norway, summer is specific for the co-presence of domestic livestock on wild reindeer grazing grounds, as for high tourist volumes, with hiking being the predominant summer use in National Parks (Gundersen et al., 2019). From the reindeer perspective, summer is very important as it is a short season to build fat reserves to survive the long winter. Moreover, in this season, calves grow to be ready for the winter too. Hence, too much disturbance or excessive use of suboptimal habitat during summer may result in poor body condition to get into winter.

All these parameters characterize the human footprint in summertime and condition related habitat loss measurements in wild reindeer ranges. Because each season is unique, both from disturbance side and from wild reindeer life-history requirements, one could expect significant differences between summer, winter and calving assessments of anthropogenic habitat loss. Accordingly, extending the current analyses to winter and calving would likely reveal different percentages of habitat loss, point out other major drivers and lead to new conclusions, thus calling for adapted disturbance management in wild reindeer ranges depending on the season. Key insights on how habitat quality and anthropogenic disturbances evolve throughout the whole annual life cycle of wild reindeer may surely arise from seasonal comparison, which is left for a future investigation in the potential continuity of this thesis.

In particular, grazing animals from agricultural livestock are absent from the mountains during winter (Colman et al., 2017), thus removing one of the main disturbances revealed to drive habitat loss in the current assessment. Furthermore, higher disturbance may be expected on winter ranges compared to summer ranges, given reindeer selection of higher elevation locations during summer, where conflicts with humans are reduced (Bergerud et al., 1990; Nellemann et al., 2001). Besides, since winter is considered the limiting season in large herbivores, given the harsh climate and scarcity of food resources (Tveraa et al., 2007), related results on anthropogenic habitat loss would be of major interest for reindeer conservation. On the other hand, increased sensitivity during the pre-calving and calving times is fairly well documented in the species' literature (Dyer et al., 2001; Vistnes et al., 2001). This could greatly strengthen avoidance at that time of the year and change results on subsequent habitat loss, especially since the current models are fed with occurrence data from adult females. Conversely, anthropogenic habitat loss may be reduced during summer due to concurring insect-harassment that can partially interfere with avoidance of human disturbances (Pollard et al., 1996; Skarin et al., 2004).

2. <u>Limitations of the study</u>

Habitat selection modeling undoubtedly constitutes an appealing and powerful tool for quantifying the impact of human disturbances on species habitat through the empirical inference of disturbance parameters from occurrence data. Although being of growing importance and widespread use, these models include some limitations that are worth bearing in mind for a relevant interpretation of the results. First of all, questions of data representativeness, models precision and results reliability should all be considered when evaluating a technique (Johnson et al., 2004). The certainty of modeling results for each herd is directly dependent on the reliability and precision of the available models and the consistency of the available data. While processing these results, inherent uncertainty contained in the models must be acknowledged, as well as the data on the basis of which they were implemented. Validity of current habitat selection models was demonstrated by Panzacchi et al (2015) through goodness-of-fit and robustness assessments. Assuming the reliability of such models for predicting habitat selection in wild reindeer, selection functions were derived based on GPS data from 257 radio-collared females over a 45-day time period (July 1st – August 15th). Although covering a limited time period and despite reported sex-dependence of the avoidance response reported in wild reindeer faced with human disturbance (Cronin et al., 1998; Vistnes & Nellemann, 2008), these data were considered representative of wild reindeer habitat selection on summer grazing. However, it should be noted that correlational studies such as this one are limited in their ability to test the influence of individual drivers on avoidance, what then makes it more difficult to build strong causal links and requires caution in the inference. Moreover, the correlation of multiple stressors on the landscape may involves difficulties in allocating consequences to their exact source and to untangle the effects of single disturbances (Dormann et al., 2013). Therefore, this situation makes the issue of confounding factors an additional relevant point to be noticed in disturbance studies such as proposed in this thesis (Colman et al., 2017). Still, despite these limitations, the results that stems from the present modeling approach are trusted to be reliable enough for applied uses and guidance in wild reindeer management and conservation.

Besides limitations of the model itself, further limitations of the present approach are rather related to what is actually being measured by models, and what is of interest. Here, occurrence – or use – is measured and used as a proxy of habitat quality, which is certainly of interest in the context of the human footprint. Still, it would be even more interesting to link habitat quality to fitness measures. Although it may be related to fitness when animals are behaving optimally and at

sufficiently low densities, occurrence is not a fitness measure (Avgar et al., 2020). Hence, while present results clearly demonstrated the broad impact of human disturbances on wild reindeer habitat quality, whether and how this could be related to animal performances and translate into population decline still needs to be investigated. Although a fair correspondence may, to some degree, be assumed between habitat quality and animal fitness, RSF models characterize space use patterns without any explicit assumption of fitness (Boyce, 2010; Boyce & McDonald, 1999). As for all spatial modeling exercises of this kind, monitoring of the population is therefore recommended to support habitat preferences stemming from the models, and further infer on habitat-performance relationships (Boyce & McDonald, 1999; Johnson et al., 2010). In reindeer, these results on habitat quality should ideally be interpreted in light of changes in fitness-related parameters such as population size, growth trend, calves and yearlings mortality, reproduction or recruitment rates (Environment Canada, 2011). Furthermore, Gaillard and colleagues (2010) argue that traditional resource selection studies should be combined with other knowledge on life history requirements and resource use to better understand underlying drivers of habitat-performance relationships. Ultimately, we should endeavor to understand how habitat quality interacts with population performances, what may be pivotal to identify acceptable disturbance thresholds compliant with population viability, as well as to strengthen the current methodology, identify the ecological traps it contains and increase the reliance of using such models for reindeer management and conservation purposes. Thus, documenting the functional consequences of human disturbances on wild reindeer biology and population dynamics would allow for testing the hypothesis that increased human footprint on wild reindeer ranges negatively affects population performances.

In addition, several challenges still need to be tackled to improve the relevance of the present approach for further uses. One limitation of what is done here lies in the absence of time dimension in the assessment. Since the natural suitability is used as a reference to quantify anthropogenic habitat loss, current assessment actually compares today's landscape to a pristine baseline environment, free of human developments, embodied by the natural suitability. This may explain the high percentages of habitat loss (π) that were found in this study, which cannot be compared to those yielded by the QN3A assessment, neither categorized based on the same thresholds. If such thresholds were use to transpose current π values in traffic-light scores, all but one area would be classified as 'red' (bad) under the 50% habitat loss threshold from the expert-based QN3A assessment (cf. Material and Methods section on the percentage of habitat loss). This is mainly

because of key difference in baseline disturbance levels considered in the two methods. The expert-based methodology for seasonal habitat loss assessment (QN3A) uses a 50-year perspective instead of a pristine baseline environment, which makes that assessment less conservative and perhaps more encouraging for management. However, assessing habitat loss over a given period of time involves taking a disturbed landscape as a reference, and therefore requires data on baseline disturbance levels. With the model-based approach proposed here, including time perspective was not something feasible since mapping data of past human activity and infrastructure are still lacking at a sufficiently relevant level of detail to understand variations in reindeer space use in relation with human disturbances, thus raising the challenge of achieving such data in the years to come.

Furthermore, considerations may be raised on the effects of wide changes in land use on the quantification of the human footprint, given the current approach is based on a static view of the land cover. This issue is of particular importance with respect to hydropower, which is the only major land-cover conversion that affects wild reindeer in their remote living areas, where they are faced with relatively few other anthropogenic land-use changes. The establishment of hydropower reservoirs in the middle of the last century involved the large-scale flooding of mountain areas for energy production, which resulted in substantial loss of reindeer habitat in certain areas (such as Setesdal Ryfylke, pers. comm.). However, these are a challenging type of infrastructure to model the removal, as they were mostly built in areas already covered by many lakes. Therefore, simply substituting present-day reservoirs by suitable reindeer habitat for modeling would likely result in a substantial overestimation of anthropogenic habitat loss. The impact of hydropower reservoirs should therefore ideally be valued by separating the 'anthropogenic' part from the 'natural' part of the reservoirs, i.e. the former lake. Such processing would require mapping data of lakes distribution in pre-reservoir times. Unfortunately, these data are largely incomplete given that most Norwegian reservoirs were filled concurrently with first satellite records. Accordingly, hydropower reservoirs were deliberately treated as a natural variable in this study, because the resulting underestimation of the human footprint was deemed less detrimental than the massive overestimation from the opposite choice. However, remote-sensing maps on water transitions (Pekel et al., 2016, accessible from: https://global-surface-water.appspot.com/download) could provide indications on pre-reservoir water levels. In addition, in Sweden, and possibly for semi-domesticated reindeer in Norway too, additional land-use changes, such as forestry, may occur (Kivinen, 2015; Kumpula et al., 2007), leaving this consideration open for model developers.

Finally, it should be noted that the present study has only focused on habitat loss, thus overlooking the effects of habitat fragmentation. However, anthropogenic encroachment on wild reindeer habitat does not only result in habitat loss, but it also causes the loss of functional connectivity that reduces the ability of wild reindeer to move freely in the landscape and reach seasonal ranges (Beyer et al., 2016; Kjørstad et al., 2017). In particular, the acknowledgement of habitat fragmentation in the current study brings further consideration on the relation between habitat quality and habitat use. Some authors argue that in highly human-dominated landscapes, habitat fragmentation may prevent animals from accessing preferred habitats and force them to live in suboptimal locations, thus introducing bias in habitat selection modeling and subsequent inference (Gill et al., 2001; Matthiopoulos, 2003; Van Horne, 1983). Indeed, selection models rely on the assumption that individuals can freely respond to environmental variation, in order to meet their ecological requirements, by means of movements and adjusted distribution, so that occurrence is directly related to habitat quality. Hence, the current approach was based on using the probability of occurrence – or use – yielded by RSFs as a direct proxy of wild reindeer habitat quality. However, this assumption must be qualified in areas of extensive disturbance, where animal movements are limited by anthropogenic barriers. Moreover, since habitat has to be simultaneously of good quality and well connected to support reindeer, like other wildlife populations, cumulative effects of habitat loss and fragmentation should be further investigated for a better understanding of anthropogenic landscape changes and their consequences on mobile species (Carrao et al., 2019; Saura & Pascual-Hortal, 2007; Stange et al., 2019). Valuable work has been done in this regard, including research from Stange et al. (2019), on green infrastructure, or from Van Moorter and colleagues (2015, 2016, 2021), on the habitat functionality metric and the quantification of effective connectivity in landscapes. Accordingly, although concerns of habitat fragmentation clearly goes beyond the scope of this thesis, these are nonetheless essential to mention for a complete discussion and correct use of its results for management and conservation purposes. In this sense, preserving functional connectivity of high-quality habitat in southern Norway appears as a priority to conserve sustainable population units of wild reindeer in the future.

CONCLUSION AND PERSPECTIVES

In conclusion, the present human footprint study provided two major guidelines for wild reindeer management and human disturbances mitigation in its summer ranges. First, in line with objective 1 and 2 (Obj. 1, Obj. 2) results on the percentage of anthropogenic habitat loss and limiting factors of habitat quality revealed unevenly impacted herds, therefore calling for prioritized management. Then, addressing objective 3 (Obj. 3), results suggested the main sectoral and single drivers of habitat loss to vary between management areas, thus highlighting the need for targeted mitigation of herd-specific disturbance sources. Current analyses have thus proven valuable in visualizing differences between herds, comparing realized effects of single disturbance sources and mapping the spatial distribution of key habitat components such as the natural suitability or the human footprint. Such knowledge is crucial for the mitigation of anthropogenic habitat loss and the future prevention of human-reindeer conflicts. In particular, this thesis leveraged the opportunity lying in the RSFs developed by Panzacchi et al. (2015) and available wild reindeer occurrence data to assess anthropogenic habitat loss in the species summer ranges, while addressing the issue of data limitation of expert assessment in the QN3A methodology. Thus, it provides an innovative approach for the quantitative assessment and mapping of anthropogenic habitat loss in wild reindeer ranges. Both expert and RSF-based methodologies offer unique advantages for habitat loss assessment. For that reason, it is argued that present approach could improve QN3A assessment in combination with expert knowledge, which might additionally play a key role in model improvement and outputs interpretation. Accordingly, the present work will hopefully help to improve wild reindeer conservation and contribute to sustainable land-use planning in reindeer habitat, as similar research already did for endangered caribou herds in Canada (see e.g., Boulanger et al., 2012; Environment Canada, 2011; Johnson et al., 2004; Polfus et al., 2011; Sorensen et al., 2010).

Of particular importance to terrestrial wildlife management and conservation are questions of habitat loss and degradation (WWF, 2020). With many wildlife populations facing decline, understanding how human-induced landscape changes affect species habitat is a paramount requirement to tackle the current biodiversity crisis. As being a major driver of species distribution and persistence in terrestrial ecosystems, as well as the leading cause of biodiversity loss worldwide, quantification and mapping of anthropogenic habitat loss hold scientific attention. It

can be argued that studying the human footprint through habitat selection models, as illustrated in this study, is a major step in reliably identifying locations of human-wildlife conflicts and quantifying the related impacts for some biodiversity components. Therefore, the modeling of habitat quality in relation with the continuum of anthropogenic pressures on the landscape provides a strong, standardized and methodological framework for species-specific, quantitative cumulative impact assessment and human footprint mapping, which seems worth to pursue. Indeed, it could help to test for the effect of a wide range of stressors on multiple species sensitive to human disturbances that characterize our modern-day landscapes. Accordingly, the work that has been done here for reindeer could be extended and more broadly applied to a large number of species, using citizen or expert data when GPS records are limited, thus helping to tackle the loss of high-nature value ecosystems and playing a critical role in slowing down the biodiversity crisis, a pressing requirement WWF outlined in its last Living Planet Report (WWF, 2020). In this respect, I personally hope that this thesis may represent a tiny, yet significant, contribution to one of the most challenging tasks of our time, namely to bend the trend of biodiversity loss.

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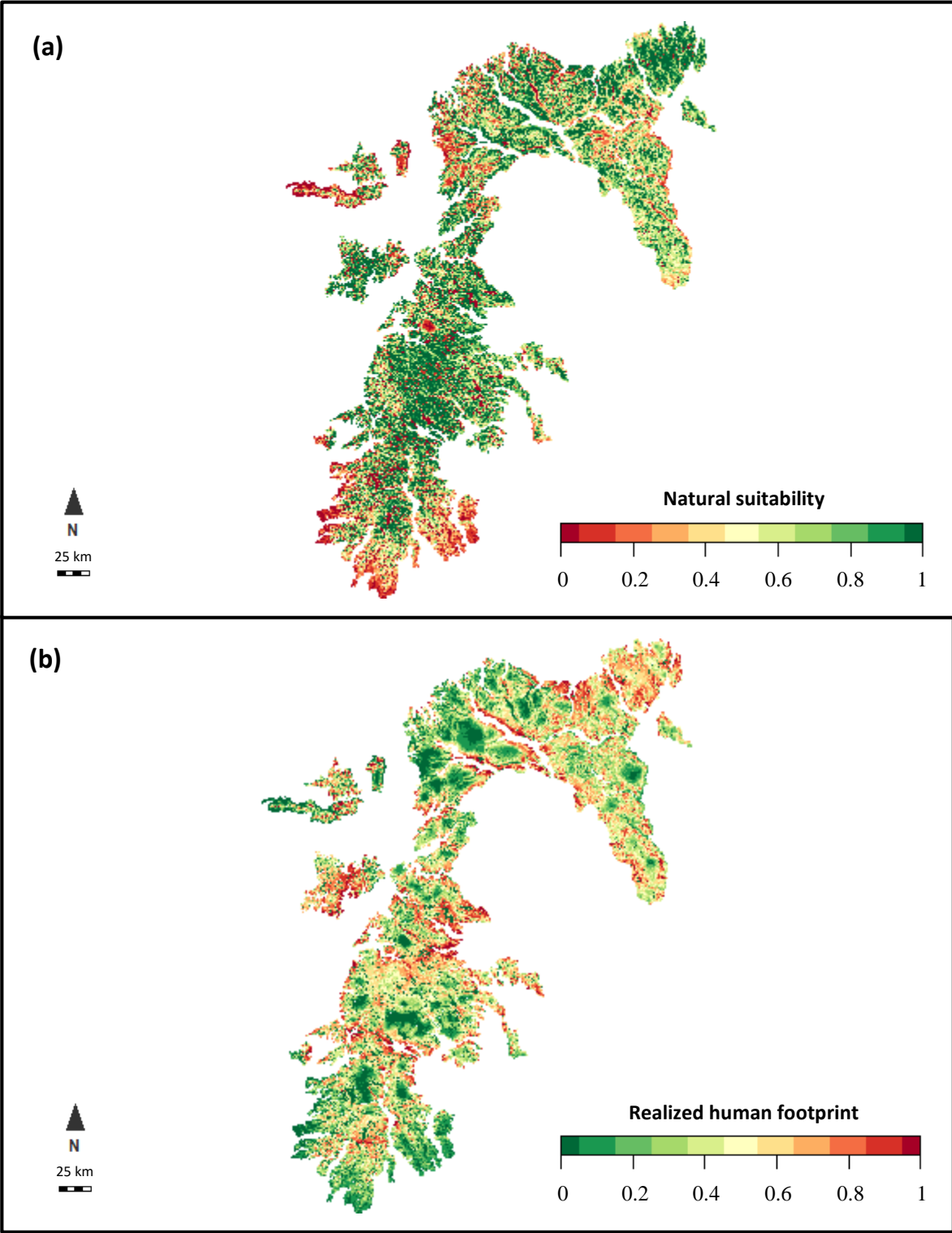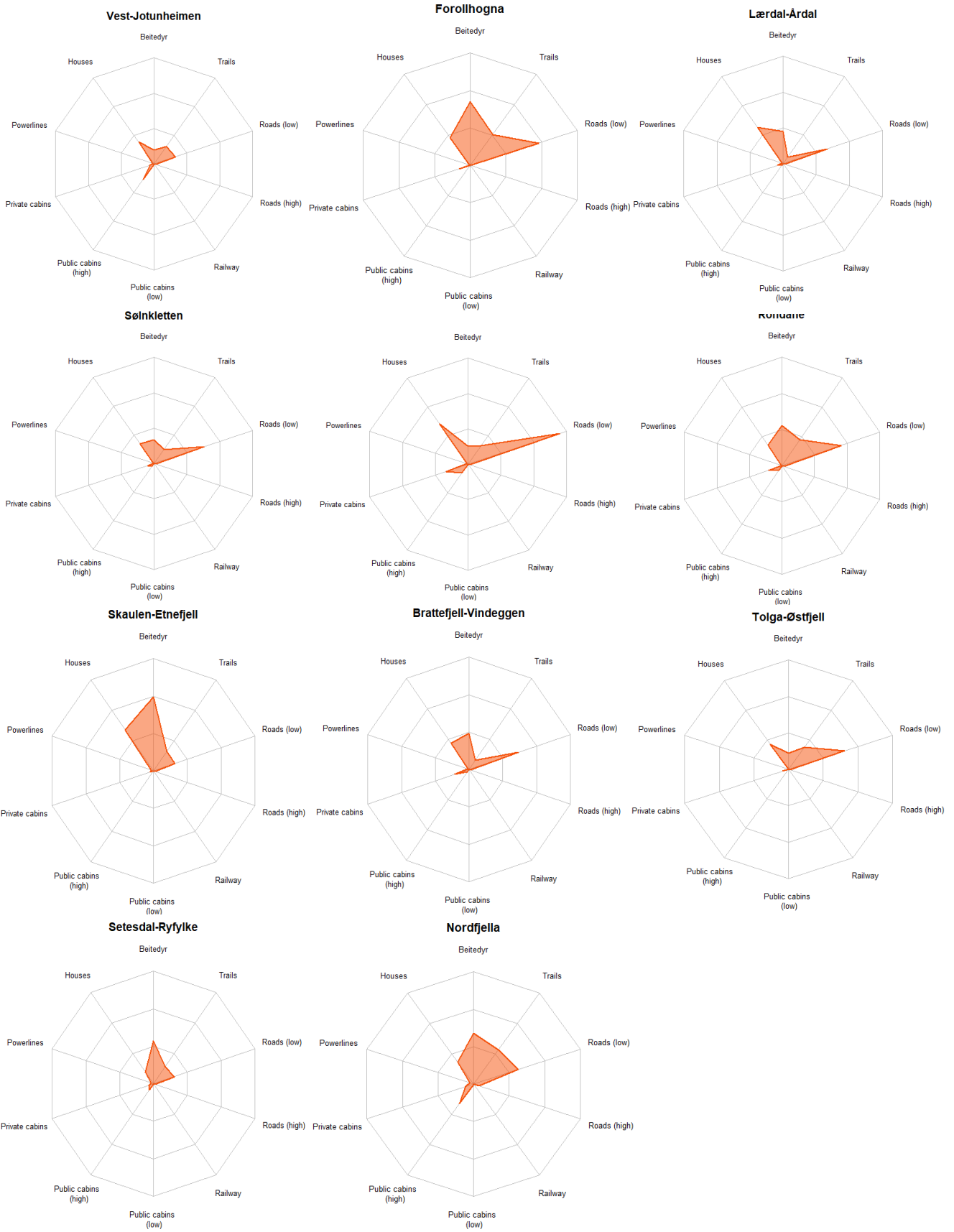
APPENDIX

Appendix 1
Spatial distribution of (a) the natural suitability and (b) the realized human footprint in the study area

Appendix 2 (part 1)

Individual radar charts showing single-driver human footprint profiles in each of the 23 wild reindeer management areas comprised in the study area.

Appendix 2 (part 2)

Individual radar charts showing single-driver human footprint profiles in each of the 23 wild reindeer management areas comprised in the study area.