



Effects of cumulated outdoor activity on wildlife habitat use

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ABSTRACT

Humans profoundly affect animal distributions by directly competing for space, not only transforming, but actively using their habitat. Anthropogenic disturbance is usually measured via structural proxies such as infrastructure and land use that overlook the impact of human presence, or functional disturbance. In this study, we propose a methodology unifying two paradigms, human mobility and animal movement, to fill this gap. We developed a novel spatially-explicit index of anthropic disturbance, the Cumulative Outdoor activity Index (COI), and validated it with ground truth observations derived from camera trapping ($r = +0.63$, $p < 0.001$). Building on previous work from Peters et al. (2015, *Biol. Cons.* 186, 123–133) on a Critically Endangered brown bear population in the Alps, we used Resource Selection Analysis to assess the influence of different forms of anthropogenic disturbance on the relative probability of habitat selection. The intensity of COI provided an effective measure of functional anthropogenic disturbance, and it outperformed all alternative and commonly-used proxies of structural disturbance in predicting bear habitat use. Our predictions suggest that brown bear shrinks its ecological niche as a consequence of intense human use of otherwise suitable habitat. These constraints may limit the potential range expansion of bears to establish a viable Alpine-Dinaric metapopulation. Conclusive conservation and future land use planning towards human-wildlife coexistence should account for the functional presence of humans on the landscape. The proposed COI could help determine where mitigation measures should be enforced.

1. Introduction

Human impact has become the most relevant determinant of animal species distribution and persistence, with the extirpation of populations and extinction of species occurring at an unprecedented rate (Ceballos et al., 2015). Alongside indirect modification of abiotic conditions (i.e., pollution, climate change) (Pecl et al., 2017), harvesting (Ripple et al.,

2016), and the introduction of invasive species (Gallardo et al., 2016), humans affect animal distribution by directly competing for space. Several methods have been applied to assess the effect of habitat fragmentation, urbanisation and connectivity loss on animal population distribution, occurrence, and space use behaviour (Compton et al., 2007; Crooks et al., 2011; Panzacchi et al., 2016; Prokopenko et al., 2017). Recently, by using the Global Human Footprint Index, Tucker et al.

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(2018) showed that mammal species moved shorter distances under high human exposure. These analyses mainly utilized structural (i.e. passive) proxies of human competition for space based on infrastructure, land use, human accessibility (e.g., linear features such as roads, land and waterways), and encroachment (e.g., population density, night-lights). However, direct competition for space should emerge by functional (i.e. active) utilisation of the aforementioned infrastructures, specifically human mobility.

Human mobility has exponentially grown in the Western world after WWII (Freund and Martin, 1993), and globally in the last 3 decades (Susilo et al., 2007). An entire branch of human geography is dedicated to the measurement and analysis of human mobility (Barbosa et al., 2018) and has been spurred by the global spread of personal tracking devices (e.g., navigation systems, mobile phones, GPS watches). Human mobility big data are analysed for many applications, from marketing (Wedel and Kannan, 2016), to traffic control (Herrera et al., 2010), and rescue services (Amin et al., 2012), which target human behaviour and space use. Only a few studies can be found that assess the impact of human mobility on wildlife, with the exception of a wide literature on traffic and roadkills (Trombulak and Frissell, 2000; Coffin, 2007; Dean et al., 2019). Beyond motorized mobility, human presence in wild habitats at the fine scale has been assessed using camera traps (Oberosler et al., 2017) or handheld tracking devices (Moen et al., 2012; Squires et al., 2019).

Recently, a diversity of mobile device software applications to track recreational outdoor activities, such as hiking, running or cycling, have become increasingly popular. In particular, the tools provided by Strava (San Francisco, CA, USA) are used worldwide to track user movements and access a crowdsourced Global Heatmap (Strava, 2018a). The Global Heatmap is a visualisation of the cumulative outdoor activity tracks recorded and marked as public by users, with monthly updates. Since its establishment as a tracking app, trajectories have been uploaded at an exponential rate, reaching over two billion records (Strava Press,

2018a), making the Global Heatmap the world's largest freely-viewable collection of GPS-tracked human outdoor activities of its kind. Strava data (Strava, 2018b) have been used for urban planning purposes or public health studies (Table S1.1). Despite this great potential, Strava-derived data have never been integrated into ecological studies.

In this work we introduce the Cumulative Outdoor activity Index (COI), a novel spatially-explicit index of anthropic disturbance based on the Strava heatmap, and used to assess active competition for space as opposed to structural indicators of anthropic disturbance (i.e., human settlements and linear features such as trails or roads). Building on previous work from Peters et al. (2015), we modelled habitat selection by a brown bear population reintroduced in the Eastern Italian Alps (Fig. 1) as a critical case study. Brown bears were reintroduced in Western Trentino in the early 2000, after the local population had been functionally extirpated, with the goal to reestablish a Alpine-Dinaric metapopulation (Duprè et al., 2000; Kaczensky et al., 2012). Despite the steady population increase in the first period after reintroduction, it did not substantially expand its range, nor was the goal to reestablish an Alpine-Dinaric metapopulation met. As a result, the Alpine brown bear population remained isolated and was listed as Critically Endangered due to the low number of mature individuals (< 50, Criteria D1; IUCN, 2001) (Huber, 2018). Conversely, human-bear conflict emerged (Gronff et al., 2019) and several bears died from anthropogenic causes (Tenan et al., 2016). We hypothesise that direct competition for space with humans has limited the selection of preferred sites within the home ranges of bears, more so than environmental restrictions and structural proxies identified in previous studies (Duprè et al., 2000; Peters et al., 2015). Given that biological processes can be observed and interpreted differently at various scales (Ciarniello et al., 2007; Mateo Sanchez et al., 2014), we considered the relative effect of anthropogenic disturbance at the home range scale (i.e., third-order selection; Johnson, 1980).



Fig. 1. Digital Terrain Model of the study area. The Adige river watershed divides the area in two sectors: Western and Eastern Trentino. The brown bear area (vertical hatching) is represented by a 95% Kernel Density Estimation of all GPS locations. The area of validation of the Cumulated Outdoor activity Index with ground truth from camera trap observations is indicated by horizontal hatching.

2. Materials and methods

2.1. Assessing functional anthropic disturbance: the Cumulative Outdoor activity Index

In order to assess the active competition for space between humans and wildlife, we developed an index measuring the effective use of structural linear features, or any portion of the habitat, through outdoor activities. For this purpose, we visualised and processed the Strava Global Heatmap (Strava, 2018a) at the highest resolution freely viewable online without registration (i.e. 20 m, or zoom level 13 OpenStreetMap Wiki contributors, 2019).

2.1.1. Strava Global Heatmap structure

The Strava Global Heatmap displays a colour gradient of outdoor activity tracks (rides, runs, water, and winter activities) recorded by users, where brighter tones (i.e., higher heat) represent an intense use, i.e. many overlapped activity tracks. Activity tracks are recorded as ‘pixel paths’ connecting consecutive GPS locations (Robb, 2017), so that the count of paths overlapping in each pixel corresponds to a raw ‘heat’ count. Such counts are then normalised to the bounded range (0,1) using a Cumulative Distribution Function (CDF), and weighted with respect to the neighbour context of intensity of use (i.e., the heat values are not comparable at a large distance, but are comparable in the proximity—about 50 km diameter at our zoom level, see below). For more technical details on how the Strava Global Heatmap is built, see Supporting information S2.

2.1.2. Deriving the Cumulative Outdoor activity Index

We derived the Cumulated Outdoor activity Index using the freely viewable Strava Global Heatmap. The approach requires few parameters and it is best achieved in a GIS environment. The extraction took place as follows: (i) an area of interest (Western portion of Trento Province, Fig. 1, and paragraph ‘Study area’) was displayed in the Strava Global Heatmap website (Strava, 2018a); (ii) we set the zoom level to 13 (OpenStreetMap Wiki contributors, 2019), the highest displayable without the need to register with a private account; (iii) we set the Heatmap Colour as “blue” (see below), the desired Activity Type to “All”, the Heat Opacity to 100%, and we removed all background layers; (iv) we took a screenshot of the displayed area and saved it as a raster PNG image; (v) we georeferenced the raster image in a GIS environment using 6 control points. We used the WGS 84/Pseudo-Mercator Coordinate system (EPSG: 3857), as it was the projected coordinate system used to build the Global Heatmap (Robb, 2017); (vi) we repeated the procedure as many times as needed to cover the entire study area, and merged all the georeferenced raster layers; (vii) we manually removed the activities overlaying ski slopes and water bodies, which were not of interest for the purpose of this study, using subtracting masks obtained from local geographic layers (Autonomous Province of Trento, 2019); (viii) we displayed single pixels as a 256-element colour spectrum array (Robb, 2017), so that when the aggregated activities are shown as “blue”, the array matches perfectly the Blue colour spectrum of an RGB colour model (0, 255); (ix) we rescaled the value so the index (COI) ranged from 0 to 1.

2.1.3. Validation of COI through ground truth observations

In order to validate the COI as an honest proxy of human use of wildlife habitats, we compared its values with human detections obtained via independent counts recorded on camera traps. In a subset of our study area (Fig. 1), an extensive, systematic camera trap survey ($n = 60$) was conducted (Oberosler et al., 2017; see Supporting information for details), recording both wildlife and human presence along forest roads and trails (30 sites in each category). Humans passages were recorded either as pedestrians/bikers or vehicles (cars, motorbikes, tractors, and trucks). We considered the former as ground truth observations, and excluded the latter as not matching the purpose of this

study. We tested the validity of the COI by comparing it with ground truth observations, measured by the number of ‘independent’ human events per site, i.e., sequential detection events separated by an interval of 1 h. First, we extracted the value of COI associated with each camera trapping site. To account for spatial imprecision, we drew a 50 m radius buffer around each trapping location and extracted the 95th percentile COI value within that buffer. We finally tested the statistical dependence between COI values and number of human detection events using Spearman’s rank correlation coefficient (Spearman’s ρ).

2.2. A case study: assessing the effect of anthropogenic disturbance on a reintroduced brown bear population

We applied our proxy for functional human disturbance, measured as cumulated outdoor activity, to evaluate habitat selection and predict probability of space use in a reintroduced population in Trentino, Central-Eastern Italian Alps. We used the same third-order Resource Selection Analysis (RSA) as Peters et al. (2015).

2.2.1. Study area and brown bear population

The study was carried out in the Province of Trento, a 6.200 km² (Fig. 1) area characterized by rugged mountainous terrain (from 65 to 3769 m a.s.l.) and covered by forests and prairies according to the altitudinal succession. Valleys are largely human-dominated (87 inhabitants/km²), with a developed network of roads and railways (density = 95 km/100 km²). The vast infrastructural system of the Adige basin effectively constitutes a connectivity barrier for many animal species, dividing the study areas into two sectors (Fig. 1). Between 1999 and 2002, 10 adult bears from Slovenia were released in the Adamello Brenta Nature Park, Italy (PACOBACE, 2010). The newly established population colonized large parts of Western Trentino. In the study period, the brown bear population estimates (2012–2018) varied from 29 to 55, as a result of a positive, albeit variable, growth rate since 2002 (Groff et al., 2019). However, the population is still listed as Critically Endangered due to the small number of mature individuals (<50, Criteria D1; IUCN, 2001) (Huber, 2018). The brown bear is currently protected under European (Habitats Directive 92/43/EEC) and Italian Laws (L. 157/92), except for the removal of bears considered as dangerous (PACOBACE, 2010).

2.2.2. Movement data

We used the GPS trajectories of animals collared between 2011 and 2019 (8 females, 4 males; Vectronic GPS–GSM collars, Vectronic Aerospace GmbH, Berlin, Germany) for a total of 21 animal/year as part of monitoring activities undertaken by the Autonomous Province of Trento (PACOBACE, 2010; Supporting information for further information on trapping and handling). The number of surveyed individuals corresponded to about 25% of the estimated yearly average of bears in the study period (about 45 bears/year; Groff et al., 2019). The trajectories were limited to non-hibernating periods and regularized at a 6-hour fix rate using the functions in the R package adehabitatLT (Calenge, 2006), excluding a-priori data collected with less frequent schedules.

2.2.3. Environmental layers

First we extracted core environmental covariates based on Peters et al. (2015), using newer spatial layers with higher resolution and accuracy where possible, including topographic variables (altitude, slope), canopy cover, and land use (cultivated lands without orchards). We used the distribution of human settlements and linear infrastructure (trails, unpaved forest roads, and main paved roads) as proxies for structural human disturbance, as well as a combined composite layer (Table S5.1). Finally, we used the newly-derived COI as a proxy of functional anthropogenic disturbance (Table 1). All raster layers were resampled to a spatial resolution of 20 m pixel size (see Supporting information S5) and were rescaled by min-max normalization to a defined range of 0 and 1.

To create the structural disturbance layers, we generated a raster

Table 1

Set of a-priori hypothesis and corresponding models to assess anthropogenic disturbance on brown bear habitat selection at the third-order of selection (within home range). Each a-priori model contained a core set of environmental variables (topography, canopy cover, land use) as predictors and in addition one or more variable(s) for testing anthropogenic disturbance.

ID	Model	Expected disturbance	Covariates
MD1	Aggregate disturbance	Influence of human settlement proximity on selection	Core model + DHS
MD2	Generic linear disturbance	Influence of generic linear infrastructure proximity on selection	Core model + DRT
MD3	Specific linear disturbance	Influence of specific linear infrastructure proximity on selection	Core model + DMR + DFR + DHT
MD4	Density of structural disturbance	Influence of infrastructure network density on selection	Core model + dRTN
MD5	Density of functional disturbance	Influence of human activity density on selection	Core model + dCOI

proximity map based on Euclidean distance of each cell to the nearest infrastructure. We then transformed the maps to exponential decays in the form of

$$sd = 1 - e^{-\alpha d} \quad (1)$$

with sd = structural disturbance, $\alpha = 0.002$ and d = distance (m) to a given linear feature (Nielsen et al., 2009). This transformation drastically reduced the effect of linear features beyond a few hundred meters, making large distances essentially irrelevant (e.g. >1500 m). The resulting values for sd range from 0 (at $d = 0$) to 1 (for large values of d). Using Eq. (1), structural disturbance layers were calculated for Distance from Human settlements (DHS), Distance from Main Roads (DMR), Distance from Forest Roads (DFR), Distance from Human Trail (DHT), and Distance from Roads and Trails (DRT) (Table S5.1). Furthermore, for both structural and functional disturbance, we computed derived spatial covariates expressing the ‘density of disturbance’ (cumulated disturbance per spatial unit). Specifically, we summed COI and the values of the raster layer combining all linear infrastructure features (roads and trails), both ranging (0,1), within a 11×11 pixel moving window (dCOI, dRTN: Table S5.1). This accounts for the spatial context around each pixel and potentially for spatial perception of disturbance by bears (~100 m; Moen et al., 2012). We performed a correlation analysis (Hinkle et al., 2003; Fig. S5.1) between all variables, thereafter building a priori models to evaluate the respective contribution of human disturbance metrics to bear habitat selection, with covariates within the same model having $|r| \leq 0.6$ (Peters et al., 2015).

2.2.4. Resource Selection Analysis

We fit a Resource Selection Function (RSF) to estimate the probability of use by bears of given resource units (Manly et al., 2002). We applied a used/available design and estimated selection within individual home ranges, i.e. third-order selection scale (Johnson, 1980). We considered GPS fixes as used locations and calculated individual bear’s annual home range by Kernel Density Estimation (Worton, 1989) using the R package adehabitatHR (Calenge, 2006). We calculated 90% fixed kernel home ranges using h_{ref} as smoothing parameters (Worton, 1989). We sampled twice as many available than GPS-based used locations to have better parameter estimates while maintaining reasonable computational times (Northrup et al., 2013). We extracted all the environmental covariates described above at each of the used and available locations.

We evaluated how anthropogenic disturbance influences space use behaviour of brown bears in Western Trentino by testing five alternative hypotheses, corresponding to a set of a-priori RSF models (“Models of Disturbance”, MD; Table 1). Specifically, a core environmental model

with slope, TCD and CORINE land cover as predictors (to represent respectively topography, canopy cover and land use effects) was complemented by one or more variables describing different aspects of structural disturbance (DHS, DMR, DFR, DHT, DRT, dRTN; giving models MD1 to MD4, Table 1). Similarly, we complemented the core model with the index of functional anthropogenic disturbance dCOI (model MD5, Table 1). We thus fitted each RSF model using a Generalized Linear Mixed Model (GLMM) with a binomial error distribution via maximum likelihood, using a Laplace approximation. We included all the covariates as additive fixed terms and individuals as random intercept to account for autocorrelation (Gillies et al., 2006), as the purpose of this study was to quantify population-level variations as a response. We performed model selection using the Akaike Information Criterion (AIC).

We predicted the relative probability of use based on selection coefficients of the best fitting model for all pixels in the given area (Fig. 1) using the function *predict* in the R package raster (Hijmans, 2017). Afterwards, we tested the predictive capability of the RSF model via 10-fold cross-validation (Boyce et al., 2002), measuring the performance of the spatially explicit predictions with the set of random training and test subsets using Spearman’s rank correlation coefficient. We managed, processed, and analysed the data entirely on the free and open-source software QGIS 3.4.4 (QGIS Development Team, 2019), GRASS 7.4 (GRASS Development Team, 2018), and R 3.4.3 (R Core Team, 2017) under Ubuntu 16.04.3 LTS (Canonical Ltd., London, United Kingdom). Results were reported in tables created with the R package stargazer (Hlavac, 2018).

3. Results

3.1. Validation of COI as an index of functional human disturbance

The camera trap survey yielded 1262 independent events of humans both as pedestrians/bikers over a period of 30 consecutive days across the 58 camera traps that functioned well. Of these events, 514 were recorded on trails and 748 on unpaved roads. The median count of people per camera was 21.76 (IQR 2.25 to 33.50, range 0 to 108), while the median of the extracted COI values per camera was 0.08 (IQR 0.00 to 0.39, range 0 to 0.71). We found a positive, statistically significant Pearson correlation between the Cumulated Outdoor activity Index and the number of human detection events ($r = +0.63$, $p < 0.001$; Fig. S6.1).

3.2. Anthropogenic disturbance effect on bear habitat selection

Within their home range (mean home range size = 259.51 km², with IQR 40.50 km² to 313.43 km²; see Supporting information S7 for details), bears selected for steep areas and high canopy cover and strongly avoided areas with high density of functional disturbance according to the newly developed COI (most parsimonious model: MD5, Table 2; $b_{dCOI} = -5.048$, $p < 0.001$). Importantly, the effect size of dCOI was considerably larger than any other predictor in the candidate models. Still, most predictors indicating habitat disturbance showed a significant (and often strong) effect in less supported, alternative models. Bears avoided proximity to human settlements (MD1: $b_{DHS} = 2.584$, $p < 0.001$; $\Delta AIC = 97$ with respect to the best model; Table 2) and areas with high density of structural disturbance, parameterized in the models by the density of roads and trails (dRTN) (MD4: $b_{dRTN} = -2.587$, $p < 0.001$; $\Delta AIC = 328$ with respect to the best model; Table 2). When considering the influence of specific linear disturbance (MD3, $\Delta AIC = 362$ with respect to the best model; Table 2), the bear showed quite different responses, avoiding areas in proximity to main roads ($b_{DMR} = 0.935$, $p < 0.001$), but selecting for human trails ($b_{DHT} = -0.198$, $p < 0.001$). Interestingly, bears did not seem to either avoid or select forest roads ($b_{DFR} = 0.057$, $p > 0.05$). The predictors of the core model maintained similar coefficients in all models (Table 2), with the exception of cultivated lands without orchards (AGR), not significant in some models and

Table 2

Output of the set of a-priori models to assess anthropogenic disturbance on brown bear habitat selection at the third-order of selection (see Table 1 for the set of models). The estimated coefficient values (b), the 90% Confidence Interval, and the P-values (* $p < 0.01$) are reported for each covariate. The models are sorted from left to right based on increasing AIC scores (reported at the bottom).

	Model					
	MD5	MD1	MD4	MD3	Core	MD2
Slp	2.054* (1.885, 2.223)	2.394* (2.228, 2.559)	2.316* (2.149, 2.482)	2.440* (2.273, 2.608)	2.626* (2.463, 2.789)	2.610* (2.443, 2.776)
TCD	0.831* (0.759, 0.903)	0.840* (0.768, 0.912)	0.894* (0.822, 0.966)	0.924* (0.843, 1.005)	0.813* (0.742, 0.884)	0.825* (0.749, 0.900)
AGR	0.237* (0.129, 0.345)	0.183* (0.075, 0.291)	0.028 (-0.077, 0.133)	0.225* (0.115, 0.336)	-0.078 (-0.181, 0.026)	-0.070 (-0.175, 0.035)
dCOI	-5.048* (-5.430, -4.667)					
DHS		2.584* (2.364, 2.803)				
dRTN			-2.587* (-2.856, -2.319)			
DHT				-0.198* (-0.286, -0.110)		
DFR				0.057 (-0.044, 0.158)		
DMR				0.935* (0.828, 1.042)		
DRT						0.530 (-0.608, 1.667)
Constant	-1.699* (-1.810, -1.589)	-4.438* (-4.671, -4.204)	-1.879* (-1.982, -1.776)	-2.771* (-2.925, -2.617)	-2.083* (-2.182, -1.985)	-2.099* (-2.203, -1.995)
Log likelihood	-13,122	-13,171	-13,286	-13,301	-13,421	-13,420
Akaike inf. crit.	26,257	26,354	26,585	26,619	26,852	26,853

Note.

* $p < 0.01$.

marginally significant in others (Table 2). However, the core model per se was the least supported by the data than all of Models of Disturbance but MD2 (Generic Linear Disturbance). The best fitting model (MD5; Table 2) led to robust spatial predictions of the relative probability of use by brown bear in the study area (Fig. 2; average Spearman's correlation coefficient for the 10-fold cross validation: $r = +0.98$, $p < 0.001$).

4. Discussion

We demonstrated the possibility of using human movement data, as extracted from Strava Global Heatmap, to quantify functional human disturbance for wildlife over the landscape. We have provided empirical evidence that the cumulated outdoor activity influenced the space use behaviour of a Critically Endangered brown bear population (Huber, 2018). Previously, large carnivores have been shown to fear the human 'super predator' (sensu Smith et al., 2017) so that the spatial pattern of human-derived risk perception (Gaynor et al., 2019) can influence large carnivore space use (Cristescu et al., 2013; Ladle et al., 2018) and foraging behaviour (Ordiz et al., 2017). A recent human-carnivore coexistence model (Chapron et al., 2014) put forward a community ecology framework where humans are considered as an integral part of the community (Chapron and López-Bao, 2016). Our results support and integrate such a view by demonstrating that carnivore space use is not accurately portrayed when using disturbance metrics that are based solely on structural proxies of human presence (infrastructure per se). We showed that the functional use of human structures and presence (i.e. human mobility) provides a more realistic way to address the interplay between carnivore and human use of space.

4.1. Functional disturbance outperforms structural variables to predict brown bear habitat selection in Trentino

Peters et al. (2015) showed that bears selected mountainous habitat with forest cover within the home range, and avoided urban areas and linear features linked to human recreation. In this work, we integrated those results by demonstrating that bears avoided specific forms of

structural disturbance, as both density (MD4; Table 2) and proximity of man-made infrastructures (MD1, MD3; Table 2) negatively affected bear's space use. Human settlements (e.g. Nellemann et al., 2007; Martin et al., 2010; Peters et al., 2015) and paved roads (e.g. Gibeau et al., 2002; Whittington et al., 2019) had the strongest negative effect as single factors (MD1, MD3; Table 2), whereas trails were mildly attractive (MD3; Table 2), likely because they can be used by animals in moments of low human presence (i.e. night; Tattoni et al., 2015; Oberosler et al., 2017; Ladle et al., 2018). However, it was the cumulative use of landscape by people which drove bear habitat selection within their home ranges (MD5; Table 2). We referred to this effect as *functional anthropogenic disturbance*, i.e. actual human presence in the landscape. In a community ecology framework (Chapron and López-Bao, 2016), in which humans act as 'super predators' (Tenan et al., 2016; sensu Smith et al., 2017), large carnivores are expected to avoid areas with human-derived risk. If however disturbance occurs in an area of reintroduction, where a newly-established population is still at high risk of local extinction (i.e. Critically Endangered; IUCN, 2001), carnivores may not be able to avoid such risky areas. Bears in our study have demonstrated a good spatial perception of human-derived risk (sensu Gaynor et al., 2019) at the home range scale, scarcely tolerating and thus avoiding large volumes of outdoor non-motorized activities. On the other side, our findings indicate that brown bear is shrinking its ecological niche locally as a result of functional anthropogenic disturbance.

4.2. From functional disturbance to functional connectivity: landscape fragmentation from the wildlife's perspective

Metrics of structural disturbance might not be enough to fully understand the implications of human pervasiveness on animal spatial behaviour. Not only do humans consume and change the environment, but they also compete directly for space and resources. As a result, their active presence over the landscape could trigger animals' avoidance for suitable spaces (e.g. niche partitioning; Squires et al., 2019). If species have low plasticity or space is limited, direct human competition for space may have serious implications for conservation. Our application of

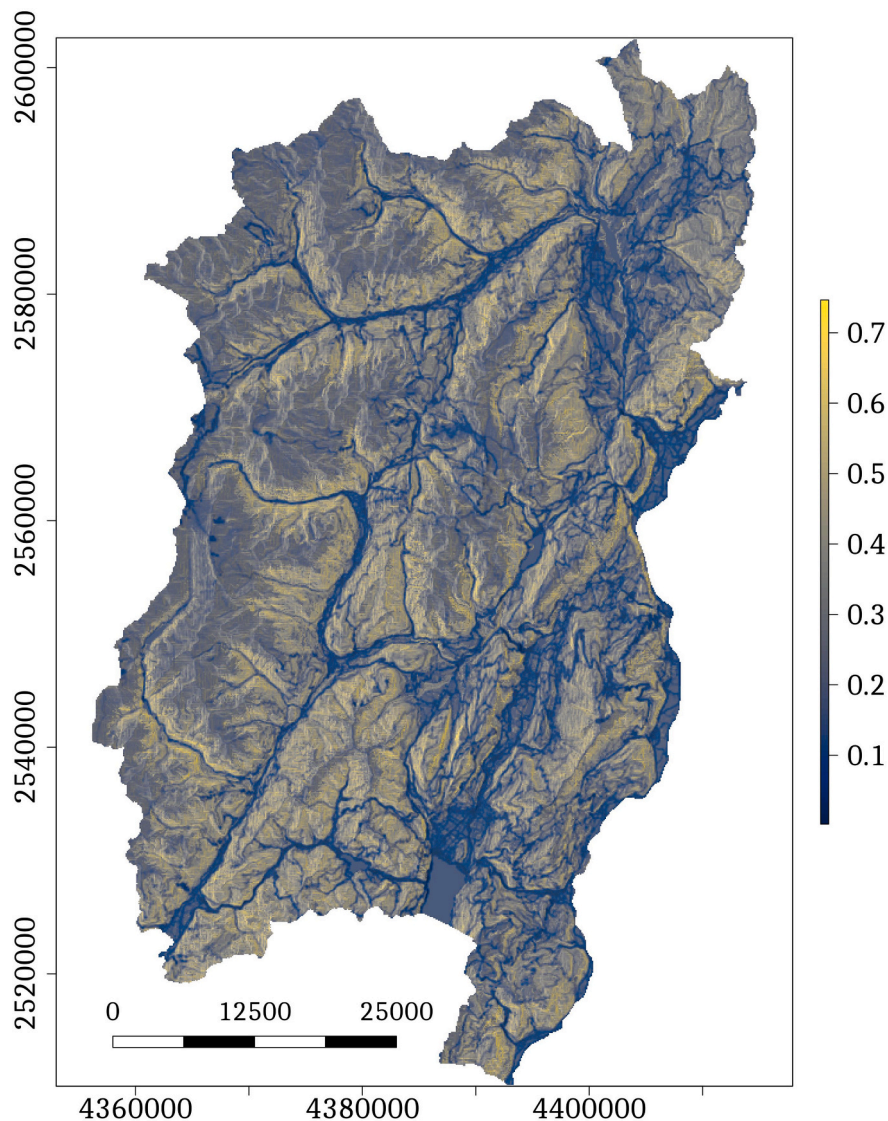


Fig. 2. Predicted relative probability of use by brown bears in Western Trentino, based on third-order (within home range) resource selection coefficients (MD5: slope, tree cover density, cultivated without orchards, density of Cumulative Outdoor activity Index). The map has a resolution of 20 m pixel size.

the community ecology-based human-carnivore coexistence model (Chapron et al., 2014; Chapron and López-Bao, 2016) by using a novel metric of functional anthropogenic disturbance indicates that conclusive conservation planning - especially in areas with high human density - should necessarily take into account human mobility. Future applications to other contexts and/or other sensitive large carnivore species (e. g. Amur Tiger, Kerley et al., 2002; Asiatic leopard, Ngoprasert et al., 2007; Iberian lynx, Fernández et al., 2003) could further generalise our findings and their implications for carnivore conservation in a world where human presence is increasingly pervasive, and the community ecology coexistence model will likely be the only viable alternative for their persistence (Chapron and López-Bao, 2016).

We were able to take and demonstrate these concepts into a concrete case of conservation concern. The predictive map (Fig. 2) showed the relative probability of brown bear habitat selection in the area of prime establishment of the reintroduced population. In general, when compared with Peters et al. (2015; Fig. 2a), areas of high probability of use seem to be more distributed, yet more fragmented. Indeed, most of the core habitat patches and linking corridors identified in Peters et al. (2015) correspond in our map to a matrix of suitable, but very small fragments. Our results seem to confirm a certain level of connectivity at the small scale, as previously predicted, but also an important

contraction of large suitable areas when we accounted for functional human disturbance. Portions with greater probability of presence were found only in the Central-South Western and Central-Northern sectors of the area, and along some narrow secondary Alpine valleys, whereas extensive human activity and large infrastructures limited the suitability of the main valley bottoms, including Adige valley (Fig. 2).

In light of these findings, the establishment of a long-term, viable Alpine-Dinaric brown bear metapopulation (Kaczensky et al., 2012) may be difficult to achieve, as potential expansion eastwards is still severely limited by both structural and functional anthropogenic disturbance. As bears continue to search for space in this increasingly complex and expanding matrix of anthropogenic disturbance, long term population viability is at risk. To facilitate this expansion, specific measures could be adopted to spatially reduce functional anthropocentric disturbance. Temporal trail/road closure, as well as seasonal restriction of areas, have shown to improve habitat quality for wildlife while still providing opportunities for human use (Lamb et al., 2018, Whittington et al., 2019). On the other hand, measures such as the establishment of recreational areas, including protected areas, could have an opposite effect to that desired, as more people would be locally drawn to outdoor activities (e. g. Fredman et al., 2007). The availability of a reliable, yet easy-to-obtain metric of functional anthropogenic disturbance, like the index we

developed, is paramount for the effective planning of such mitigation measures.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2020.108818>.

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