

Socioeconomic characteristics of suitable wolf habitat in Sweden

Fredrik Dalerum^{1,2,3}

¹ Research Unit of Biodiversity (UO-CSIC-PA), Mieres Campus, University of Oviedo, 33600 Mieres, Asturias, Spain (address for correspondence); Telephone: +34 985 10 3000 (Ext. 5927)

² Department of Zoology, Stockholm University, Sweden

³ Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, South Africa

E-mail: fredrik.dalerum@csic.es

Abstract

Large carnivores are ecologically important but their behaviour frequently put them in conflict with humans. I suggest that a spatial co-occurrence of suitable habitat and relatively poor socioeconomic conditions in rural areas may contribute to inflated human-carnivore conflict. Here, I test if there is potential for such an explanation for the human-wolf conflict in Sweden, which has a human-wolf conflict that is arguably not congruent with the costs and damages imposed by the wolf population. I found negative correlations between wolf habitat suitability within Swedish municipalities and indicators of their relative socioeconomic conditions. I argue that geographic socioeconomic inequality may contribute to the Swedish wolf-human conflict, partly by the use of wolves as symbols for socioeconomic dissent and partly by using them as scapegoats for socioeconomic conditions. Therefore, regional policies aimed at alleviating geographic socioeconomic inequities may create a more favourable environment for solving the wolf-human conflict in Sweden.

Key words Scapegoating; rural dissatisfaction; regional inequities; political dissent; large carnivore; human-wildlife conflict

Ambio 50:1259-1268

INTRODUCTION

Large carnivores are increasingly recognised for their ecological importance as well as their potential flagship values (Ray et al. 2005). Yet, they have been heavily persecuted by humans, which combined with a demographic sensitivity to additive mortality has led to substantial extinctions and declines through the late Pleistocene and the Holocene (Dalerum et al. 2009). Preserving viable populations of our remaining large carnivores has therefore risen as an important task for conservation biology (Gittleman et al. 2001). Their large area requirements makes conservation exclusively on protected land challenging (Finnegan et al. 2020), and recent population expansions in highly populated areas in Europe (Chapron et al. 2014) and India (Athreya et al. 2013) highlight that carnivore conservation may benefit from focusing on how to maintain viable populations of these species also outside of protected areas. Such a focus would also be aligned with recent suggestions that we broadly need to align human societies with the ecological realities we rely on (Mace 2014).

Co-existence between humans and large and potentially intrusive wildlife species does, however, often lead to human-wildlife conflicts (Frank et al. 2019). For large carnivores, conflict may arise from damages to livestock or property (van Eeden et al. 2017), from direct perception of fear for human lives and safety (Dickman 2010), as well as from less obvious reasons not directly related to any damages or risks (Madden 2004). Conflict directly associated with physical damages, or the risk of such damages, is at least conceptually easy to address. Possible solutions may include damage mitigation strategies, financial compensation schemes, or local or regional eradication or population suppression (Bautista et al. 2019). Human-wildlife conflict is, however, often not directly associated with either real or perceived damages or inconveniences (Treves and Karanth 2003). In contrast to conflict based on real or perceived damages, such seemingly irrational conflicts are substantially more complex to solve (Treves and Bruskotter 2014).

Attitudes towards large carnivore conservation are often polarised, with favourable attitudes towards large carnivores being contrasted by arguments for local eradication based on economic costs and declines in the quality of lives caused by their presence (Treves and Karanth 2003). This contrast in attitudes follows, to a large extent, a geographic rural-urban gradient, where urban residents in general are more favourable towards carnivores than rural ones (e.g., Røskaft et al. 2007; Frank and Sjöström 2007). This geographic gradient in attitudes is logical in situations when the direct costs of carnivores are only imposed on the rural residents that live close to them (Dressel et al. 2015; Jordan et al. 2020). However, it is harder to explain when adverse attitudes towards carnivores in rural areas appear not to be directly related to the damages they cause. Variation in attitudes have been attributed to historical, cultural, geographic and social factors (Pooley et al. 2016), which may help explaining adverse attitudes towards carnivores in the absence of real inconveniences (Treves and Bruskotter 2014).

Current economic paradigms have lead to a rapid global urbanization, which in many places has been accompanied by a social and economic depreciation of rural communities relative to urban ones (Moretti 2012). I suggest that a geographic co-variation between areas that are suitable for carnivores and such depreciation in rural socioeconomic conditions may contribute to adverse attitudes towards large carnivores in rural areas. Subsequently, such geographic co-variation could also be partly responsible for the ongoing human-carnivore conflict. This could occur through two obvious mechanisms (Fig. 1). First, relative regional inequities in economic and social prosperity often lead to social and economic dissatisfaction in rural areas (Iammarino et al. 2018). This could cause adverse attitudes towards carnivores either if they are used as a symbol for the system that is viewed to have caused the socioeconomic issues or if they are used as scapegoats, i.e. they are directly projected as potential causes for socioeconomic problems and inequities, by similar mechanisms as those that have been suggested to explain other forms of social prejudices (Harle 2000). Second, a spatial correlation between large carnivore presence and social and economic conditions would mean that the actual costs of damages or inconveniences caused by large

carnivores are carried by the members of society that are least well equipped to pay for them (Dressel et al. 2015). Recent recognition of this problem has, for instance, led to suggestions of the implementation of cost sharing as an important stepping stone towards human wildlife-conflict resolution at international scales (Jordan et al. 2020).

Sweden is a welfare state in northern Europe which hosts four large carnivore species, of which wolves are by far the most conflict prone (Sandström et al. 2015). The human-wolf conflict in Sweden is intense, and includes widespread illegal hunting which can not be directly explained by an economic need to reduce damages (Liberg et al. 2011;). I suggest that adverse attitudes towards wolves in Sweden may be, at least to some extent, caused by a geographic co-variation between suitable wolf areas and relative socioeconomic conditions. To evaluate the potential for such an explanation, I used projections of wolf habitat suitability from a previously developed environmental niche model combined with public data on economic, education, voting and demographic variables of Swedish municipalities to relate the spatial variation in suitable wolf habitat to relative socioeconomic conditions of municipalities. I also contrasted the socioeconomic conditions of areas previously identified as suitable for wolf range expansion among Sweden's three management regions.

METHODS

Study region

Sweden covers a land area of 438 600 km² and stretches from 55° 20 N to 69° 03 N. A major part of the country, approximately 70%, is characterised by mostly commercial forest. Built up areas cover only 3% and approximately 7% of the land area is used for agriculture (Statistics Sweden 2020). Human population is currently 10.3 million people, giving an average density of 23.5 people/km². However, the population is unevenly distributed with the southern parts as well as urban centres along the east coast having substantially higher densities than the national average. Sweden's climate is cold continental, with mean annual temperatures of 10°C in southern and 8°C in northern Sweden.

Sweden is administratively divided into 21 counties, which are further administratively divided into a total of 290 municipalities. Each county has a regional representation of the government in the form of a county board, directed by an appointed governor, and are managed by an elected regional council. The municipalities are managed by an elected municipal assembly. Despite these regional and local administrative structures, Sweden has a strong central administration where the national government and the Parliament define the frameworks within which regional and local administrations are allowed to operate (Stegmann McCallion 2016). The budgetary system is distinctly top-down, where the national government proposes a budget that needs to be approved by the Parliament before it is passed on to lower administrative levels.

Although each county has some autonomy in terms of large carnivore management policies, regional policies need to adhere to national guidelines. In addition, to enhance coordination of carnivore management across larger spatial scales than counties, the government has formed three management regions with a tight coordination of policies among counties within each region . The northern management region consists of Norrbotten, Västerbotten, Västernorrland and Jämtland, the central of Dalarna, Gävleborg, Örebro, Stockholm, Uppsala, Värmland, Västmanland and Västra Götaland, and the southern of Blekinge, Halland, Jönköping, Kalmar, Kronoberg, Östergötland, Skåne and Södermanland. The county of Gotland is an island in the Baltic Sea with no large carnivore presence and is hence excluded from these management regions. The municipalities do usually not form their own carnivore management policies, but adhere to the county boards regulations. About half of Sweden's land area, from the central parts and northwards, is defined as a reindeer grazing zone. This area can be utilized for semi domesticated reindeer husbandry by the native Sámi people and has, until recently, been actively excluded from potential wolf range through national policies (Eriksson and Dalerum 2018).

Socioeconomic data

I downloaded socioeconomic data for all Swedish municipalities from Statistics Sweden (<https://www.scb.se/en/api>). I targeted data that describe the general demography (population density, average age and life expectancy), household economy (median income, Gini coefficient of income, proportion of residents with low income standard), reliance on social benefits (reliance on unemployment benefits, reliance on social benefits other than unemployment), voting participation, education, as well as temporal change in population and income (Table 1). I only used data from the past 20 years, and only included variables that had a minimum of 5 years of data for all municipalities. The socioeconomic data are available in Electronic Supplementary Material, Table S1.

Estimates of wolf habitat suitability and predicted expansion areas

I used spatial predictions of probability of wolf range from a previously developed environmental niche model for Swedish wolves, fitted using MaxEnt algorithms, as estimates of wolf habitat suitability (Eriksson and Dalerum 2018). The model used wolf observations during the period 2000 to 2015 and a series of environmental variables as predictors, the most influential being the reindeer husbandry area (contributing with 56.1% to the spatial resolution of the model), forest cover (14.9% contribution), precipitation (9.7% contribution), cattle density (9.5% contribution), NDVI (3.3% contribution), density of small roads (3.1% contribution) and elevation (2.3% contribution). The model had a resolution of 20 x 20 km. Full details of the model and its parameters are given in Eriksson and Dalerum (2018). The model output was presented as a complementary log-log projection of the raw model output, which can be interpreted as a probability of range occurrence (Phillips et al. 2017).

I used 20 x 20 km cells that had previously been identified as suitable wolf range expansion areas (Eriksson and Dalerum 2018). These were cells that were binary classed as suitable wolf habitat but lied outside of current wolf range in Sweden, indicated by an absence of recorded wolf observations during 2000-2015. Suitable wolf habitat for the identification of range expansion areas had been identified from a similar MaxEnt model as described above, except that the reindeer husbandry area had been omitted as a predictor (Eriksson and Dalerum 2018).

Data analyses

Principal component analyses

I used a principal component analysis (PCA) to collate the information in the socioeconomic variables into orthogonal dimensions describing the socioeconomic conditions of Sweden's municipalities. PCA is a standard statistical exploratory technique that is carried out by doing a series of eigenvalue decompositions of a covariance matrix to find uncorrelated indices that best describe the variation in the data. Here, I used these indices as indicators of socioeconomic conditions that captured different aspects of the conditions in municipalities. To approximate normality, I logit transformed voting participation, social benefits and unemployment benefits (Warton and Hui 2011) and log transformed density, median income, and the Gini index. All variables were scaled to unit variance and centred around the mean prior to being entered into the analyses.

I used linear models fitted using generalised least squares algorithms to relate average wolf habitat suitability in Swedish municipalities to their score in the first two principal components. I used logit transformed wolf habitat suitability as response (Warton and Hui, 2011), and the two-way interactions between management region and the score of each PCA dimensions as predictors. I added a Gaussian spatial correlation structure, calculated on the geographic centroid of each municipality, to account for spatial autocorrelation. Since wolves have been actively excluded from the area designated for reindeer husbandry by the native Sámi, which corresponds to the northern

management region and the very northernmost part of the central region (Eriksson and Dalerum 2018), I only included data from the southern and central region that fell outside of this designated area.

I used mixed linear models to contrast the PCA scores of the first two dimensions in 20 x 20 km cells previously identified as suitable wolf range expansion areas between the three management regions. I created a separate model for each PCA dimension. In the models, I used the PCA score of each cell as the response variable, region as a three level factor as a fixed predictor, and municipality as a random grouping factor. I also added a linear spatial correlation structure, calculated on the central coordinate of each cell, to account for spatial autocorrelation. Pairwise comparisons were calculated using t-tests on regional means of municipalities weighted by respective number of cells identified as suitable range expansion, controlling the false discovery rate according to Benjamini and Hochberg (1995).

All statistical analyses were conducted using the statistical software R, version 3.6.3 compiled for the Linux environment (<http://www.r-project.org>). Principal component analyses were carried out using functions in the user contributed package FactoMineR (version 2.3, Lê et al. 2008) and linear and mixed linear models were fitted using algorithms in the user contributed package nlme (version 3.1-145, Pinheiro et al. 2020).

RESULTS

The first PCA dimension described 55.7 % of the variation among municipalities in the socioeconomic conditions, and the second dimension described 13.4 % (Fig 2a). Scores of the first PCA dimension were negatively related to social and unemployment benefits, percent of residents with low income standard and average age, and positively related to all other socioeconomic characteristics. Scores of the second PCA dimension were negatively related to income change, voting participation and average age, and positively related to all other socioeconomic characteristics except average income and life expectancy (Fig 2b). Social benefits, percent of residents with low income standard, median income, and percent of residents with university education had the highest contribution to the first PCA dimension, whereas population density, population change and income change contributed the most to the second PCA dimension (Table 1). Municipalities in the southern and particularly the central management region showed a large variation in their socioeconomic conditions quantified as scores of the first two PCA dimensions, but municipalities in the northern region had consistently poorer conditions quantified as scores of the first PCA dimension (Fig 2c). Municipalities in the interior northern parts of Sweden generally had relatively poor socioeconomic conditions quantified as scores of the first two PCA dimensions, and municipalities in the interior of southern Sweden had relatively poor socioeconomic conditions quantified as scores of the second PCA dimension (Fig 3a,b).

Suitable wolf habitat were primarily identified in the north, central and western parts of the central management region (Fig 3c). There were significant negative relationships between average wolf habitat suitability in municipalities and their socioeconomic conditions quantified as scores of the first (southern region: $\beta = -0.12$, $SE_{\beta} = 0.05$, $p = 0.02$; central region: $\beta = -0.30$, $SE_{\beta} = 0.03$, $p < 0.01$) (Fig 4a,b), and the second PCA dimension ($\beta = -0.27$, $SE_{\beta} = 0.08$, $p < 0.02$) (Fig 4c), indicating that municipalities which contained suitable wolf habitat also had relatively poor socioeconomic conditions. However, for scores of the first PCA the relationship was stronger in the central than in the southern management region ($\beta = 0.17$, $SE_{\beta} = 0.06$, $p < 0.01$), whereas the relationship did not differ between the southern and central regions for scores of the second PCA dimension ($\beta = -0.07$, $SE_{\beta} = 0.11$, $p = 0.53$).

Among 20 x 20km cells previously identified as suitable for wolf range expansion, there was a significant effect of management region on socioeconomic conditions quantified as scores from both the first ($F = 35.08$, $df = 2$, 207, $p < 0.01$, Fig 5a) and the second PCA dimension ($F = 29.65$, $df = 2$, 207, $p < 0.01$, Fig 5b). Quantified from scores of the first PCA dimension, cells in the

southern management region were located in municipalities with better socioeconomic conditions than cells in both the central ($t = 6.03$, $df = 134$, $p_{adj} < 0.01$) and the northern ($t = 7.49$, $df = 63$, $p_{adj} < 0.01$) management regions, and cells in the central management region were located in municipalities with better socioeconomic conditions than those in the northern region ($t = 2.46$, $df = 81$, $p_{adj} = 0.02$). Quantified from scores of the second PCA dimension, cells in the northern management region were located in municipalities with poorer socioeconomic conditions than cells in both the southern ($t = 5.61$, $df = 109$, $p_{ad} < 0.01$) and central regions ($t = 5.98$, $df = 108$, $p_{ad} < 0.01$), whereas cells in the southern and the central management regions were not located in municipalities with significantly different socioeconomic conditions ($t = 0.89$, $df = 149$, $p_{ad} = 0.37$).

DISCUSSION

My analysis shows that Swedish municipalities that had suitable wolf habitat were also characterised by relatively poor socioeconomic conditions, indicated by low income relative to the country average, a high reliance on social benefits, low levels of university education, low voting participation, low life expectancy, and a high average age. I suggest that these socioeconomic characteristics have generated a situation of social, economic and political discontent in these municipalities, which has partly manifested itself in adverse attitudes towards wolves. Plausible mechanisms for how such discontent may have generated adverse attitudes is the use of wolves as symbols for dissent, which has previously been suggested as a motivation for illegal wolf hunting (Pohja-Mykrä 2016; von Essen and Allen 2017; Skogen and Kränge 2020), and as scapegoats, i.e. partly blaming the wolves for the relatively poor rural socioeconomic conditions (Kellert 1996; Lopes-Fernandes et al. 2015). The use of wolves as a symbol in a broader regional struggle would imply that the conflict may not be rooted in any relationships between wolves and humans at all. Therefore, potential solutions may need to be looked for outside the arena of wildlife and environmental management. Such coupling of socioeconomic conditions and spatial occurrences of wildlife could explain the seemingly irrational nature of many human-wildlife conflicts (e.g., Treves and Karanth 2003). Hence, although some dimensions of the Swedish human-wolf conflict may be addressed by adjusting management mechanisms to enable a greater stakeholder empowerment (Hansson-Forman et al., 2018), I argue that geopolitical decisions aimed at minimizing a rural-urban gradient in socioeconomic prosperity may create a more favourable environment for solving the current human-wolf conflict in Sweden.

Rural dissatisfaction may take many forms, such as support for populist political movements and declined support for international institutions (Dijkstra et al. 2018). I suggest that the Swedish wolf conflict may be best viewed in this context, and regarded as an additional sign of rural dissatisfaction rather than as a distinct conflict between humans and a species of wildlife or how it is managed. In Sweden, the wolf belongs to a set of species that are owned and managed by the state. Hence, government dictates management policies, which are specified by the national Environmental Protection Agency and carried out by regional county boards. Therefore, it would not be surprising that this species, which is prone to cause very polarized attitudes across its range (Mech 2017), has been taken as a symbol for the central authority in a regional struggle between rural communities and the central government and their agencies (e.g., Eriksson 2017). The results are aligned with previous findings of economic advantages of metropolitan regions relative to rural areas in Sweden (Bjerke and Mellander 2017). I therefore suggest that there may be a broad socioeconomic context to this dissent, and that it probably reflects rural dissatisfaction at large. Such an interpretation would contrast previous studies of the role of dissent in the Scandinavian wolf conflict, which have mainly focused on environmental management dissent (Pohja-Mykrä 2016; von Essen and Allen 2017; Skogen and Kränge 2020).

In addition to expression of dissent, scapegoating is a mechanism in which dissatisfaction could lead to adverse attitudes towards wild animals, i.e. they are unfairly blamed for real or perceived problems (Sollund 2015; Dickman and Hazzah 2016). Scapegoating is a well-known

social phenomenon in which an outgroup is unfairly blamed for the misfortunes of an ingroup (Allport 1954). Such mechanisms have been suggested for adverse attitudes towards wolves throughout its range, including in Portugal (Lopes-Frenandes et al. 2015), the USA (Kellert 1996), and Japan (Knight 2003). Several observations partly support the role of wolves as scapegoats in rural areas of Sweden. For instance, fear of wolf attacks on humans or pets have been identified as one component in the perceived negative effect of wolves on rural life quality (Sjölander-Lindqvist 2009). Yet, such fear is largely unjustified (as in the case of attacks on humans, Linnell et al. 2003) or not related to wolf population density (as in the case of attacks on dogs, Dalerum et al. 2020). Scapegoating is a complex issue to solve, but information, education and participatory campaigns have been advocated as solutions in social contexts (Herch 2013). It is likely that similar methods may be successful to resolve these dimensions also for wolves. Nonetheless, long-term solutions require that the socioeconomic issues that are blamed on the scapegoats ultimately need to be addressed.

A correlation between carnivore presence and low socioeconomic standard could also lead to a situation where the costs of hosting carnivore populations are carried out by the most economically vulnerable. Despite the observed correlation between wolf range suitability and relative socioeconomic conditions in Sweden, I argue that such economic vulnerability likely has had a limited effect on the Swedish wolf conflict. Sweden is frequently ranked as one of the most prosperous countries on the planet (Conceição 2019), and even households in the most socioeconomically challenged areas are far above an economic and material standard that could lead to humanitarian issues. Additionally, although there may be some economic costs of local carnivore populations (Pedersen et al. 2019), the marginal costs of wolf expansion have been estimated as relatively low (Bostedt and Grahn 2008). Hence, I find it unlikely that the Swedish wolf population has caused significant economic hardships in rural regions. However, despite its prosperity, economic and social inequality is increasing in Sweden (Conceição 2019). Since perceived economic welfare is relative to the socioeconomic environment in which a person lives (Duesenberry 1949), I suggest that the relative socioeconomic contrasts between rural and urban areas, combined with local economic costs of wolves, may contribute towards potential feelings of victimization and political dissent (e.g., Pohja-Mykrä 2016; Eriksson 2017; von Essen and Allen 2017). The most favourable attitudes towards wolves have also been observed among those who do not carry any direct costs of living close to them (Frank and Sjöström, 2007). Such a situation is congruent with the NIMBY (Not in My Back Yard) concept, i.e. local resistance to generally accepted processes (Dear 1992). The NIMBY phenomenon has been most prevalent in land use planning (e.g., Chively 2007), but it has also been suggested for contributing to attitudes towards Swedish wolves (Von Essen and Allen 2020).

In the current management plan for wolves in Sweden, all historically inhabited areas are to be regarded as potential wolf range (Naturvårdsverket 2016). This is a distinct policy shift compared to previous wolf policies in Sweden, since the Swedish wolf population earlier was excluded from the area defined as the reindeer grazing zone (Eriksson and Dalerum 2018), an area which largely overlaps with the northern management region. The reindeer grazing zone is used by the native Sámi culture to host semi-domestic reindeer. While a commercial activity, reindeer herding is also a central culture carrier for the Sámi minority (Bostedt and Lundgren 2010). Reindeer herding is particularly sensitive to disturbance by wolves, and an expansion of the wolf population into the northern parts of Sweden should only be allowed if it will not interfere with reindeer herding activities (Naturvårdsverket 2016). Even if wolf establishments are achieved without disturbance to Sámi communities, my results indicate that they may not be without social friction. Municipalities in the northern management region consistently scored lower in both of my initial PCA dimensions, which indicate lower socioeconomic standards, than counties in central and southern Sweden. Therefore, even if conflict with reindeer herding activities were to be largely avoided, I suggest that a wolf expansion into the northern part of Sweden may still need to be

accompanied by significant information programs aimed at limiting the social components of the wolf-human conflicts. Limiting such social conflict components has been identified as important for large carnivore re-introductions (Macdonald 2009), and the socioeconomic characteristics of suitable wolf expansion areas, particularly in northern Sweden, suggest that it may be a necessary component of a management program aiming at a broad geographic distribution of the Swedish wolves.

To conclude, I found a negative spatial correlation between habitat suitability for the Swedish wolf population and socioeconomic conditions, particularly in the central parts of Sweden where the wolf population is the most dense. I therefore argue that such relative socioeconomic inequality may contribute to the Swedish wolf-human conflict, partly by the use of wolves as symbols for a broad socioeconomic dissent and partly by the use of wolves as scapegoats for relatively poor rural socioeconomic conditions. While the economic strain caused by wolves in itself may not have been influential for causing the Swedish wolf-human conflict, the relative income disparity between rural and urban areas, combined with a cost imposed primarily on rural residents, may have contributed towards feelings of victimization and political dissent. I therefore argue that regional policies aimed at alleviating a socioeconomic divide along a rural-urban gradient may create more favourable conditions for solving the Swedish wolf-human conflict. Hence, although strictly correlative, my study suggests that long-term solutions for the often complex issues surrounding human-wildlife conflicts may be found in areas not directly associated with conservation biology or environmental science. Although data are currently not available at appropriate spatial scales for wolves in Sweden, I encourage further analyses relating socioeconomic characteristics directly to attitudes towards conflict prone carnivores to establish if and how socioeconomic mechanisms may dictate human-wildlife interactions.

Acknowledgements: Maria Miranda, associate editor Wynand Boonstra and two anonymous reviewers provided valuable comments on drafts of the manuscript.

REFERENCES

- Allport, G. 1954. *The Nature of Prejudice*. Boston: Addison-Wesley.
- Athreya, V., Odden, M., Linnell, J.D., Krishnaswamy, J. and Karanth, U. 2013. Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PLoS One* 8:e57872.
- Bautista, C., Revilla, E., Naves, J., Albrecht, J., Fernández, N., Olszańska, A., Adamec, M., Berezowska-Cnotaa, T., Ciucci, P., Groff, C., Härkönen, S., Huber, D., Jerina, K., Jonozovič, M., Karamanlidis, A.A., Palazón, S., Quenette, P.Y., Rigg, R., Seijas, J., Swenson, J.E., Talvi, T. and Selva, N. 2019. Large carnivore damage in Europe: Analysis of compensation and prevention programs. *Biological Conservation* 235:308-3016.
- Benjamini, Y. and Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B* 57: 289-300.
- Bjerke, L. and Mellander, C. 2017. Moving home again? Never! The locational choices of graduates in Sweden. *The Annals of Regional Science* 59:707-729.
- Bostedt, G. and Grahn P. 2008. Estimating cost functions for the four large carnivores in Sweden. *Ecological Economics* 68:517-524.
- Bostedt, G. and Lundgren, T. 2010. Accounting for cultural heritage - A theoretical and empirical exploration with focus on Swedish reindeer husbandry. *Ecological Economics* 26:217-226.
- Burnham, K. 2000. Using the Language of NIMBY: A topic for research, not an activity for researchers. *Local Environment* 5:55-67.
- Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., André, H., López-Bao, J.V. et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346:1517–1519.

- Chively, C. 2007. Understanding the NIMBY and LULU phenomena: Reassessing our knowledge base and informing future research. *Journal of Planning Literature* 21:255-266.
- Conceição, P. (ed.) 2019. *Human Development Report 2019. Beyond income, beyond averages, beyond today: Inequalities in human development in the 21st century*. New York: United Nations Development Program.
- Dalerum, F., Cameron, E.Z., Kunkel, K.E. and Somers, M.J. 2009. Continental patterns of carnivore guild depletions: Implications for prioritizing global carnivore conservation. *Biology Letters* 5:35-38.
- Dalerum, F., Selby, L. and Pirk, C.W.W. 2020. Relationships between large carnivore population density and live-stock damages in Sweden. *Frontiers in Ecology and Evolution* 7:507.
- Dear, M. 1992. Understanding and overcoming the NIMBY syndrome. *Journal of the American Planning Association* 58:288-301.
- Dickman, A. 2010. Complexities of conflict: The importance of considering social factors for effectively resolving human-wildlife conflict. *Animal Conservation* 13:458-466.
- Dickman, A.J. and Hazzah, L. 2016. Money, myths and man-eaters: Complexities of human-wildlife conflict. In *Problematic Wildlife: A Cross-Disciplinary Approach*, ed. Angelici, F.M., 339-356. New York: Springer.
- Dijkstra, L., Poelman, H. and Rodríguez-Pose, A. 2018. *The Geography of EU Discontent*. European Commission Working Paper 12/2018. Luxembourg: Office of the European Union.
- Dressel, S., Sandström, C. and Ericsson, G. 2015. A meta-analysis of studies on attitudes toward bears and wolves across Europe 1976-2012. *Conservation Biology* 29:565-574.
- Duesenberry, J.S. 1949. *Income, Saving and the Theory of Consumer Behaviour*. Cambridge: Harvard University Press.
- Eriksson, M. 2017. Political alienation, rurality and the symbolic role of Swedish wolf policy. *Society & Natural Resources* 30:1374-1388.
- Eriksson, T. and Dalerum, F. 2018. Identifying potential areas for an expanding wolf population in Sweden. *Biological Conservation* 220:170-181.
- Finnegan, S., Galvez-Bravo, L., Silveira, L., Tôrres, N. M., Jácomo, A. T., Alves, G. B. and Dalerum, F. 2020. Reserve size, dispersal and population sustainability of wide ranging carnivores: the case of jaguars (*Panthera onca*) in Emas national park, Brazil. *Animal Conservation* Online early doi:10.1111/acv.12608
- Frank, J. and Sjöström, M. 2007. Human attitudes towards wolves, a matter of distance. *Biological Conservation* 137:610-626.
- Frank, B., Glikman, J.A. and Marchini, S. 2019. *Human-Wildlife Interactions: Turning Conflict into Coexistence*. Cambridge: Cambridge University Press.
- Gittleman, J.L., Funk, S.M., Macondald, D.W. and Wayne, R.K. (Eds.) 2001. *Carnivore Conservation*. Cambridge: Cambridge University Press.
- Hansson-Forman, K., Reimerson, E., Sjölander-Lindqvist, A. and Sandström, C. 2018. Governing large carnivores—Comparative insights from three different countries. *Society & Natural Resources* 31:837-852.
- Harle, V. 2000. *The Enemy with a Thousand Faces: The Tradition of the Other in Western Political Thought and History*. Westport: Greenwood Publishing.
- Herch, M.A. 2013. Barriers to ethical behaviour and stability: Stereotyping and scapegoating as pretexts for avoiding responsibility. *Annual Reviews in Control* 37:365-381.
- Iammarino, S., Rodríguez-Pose, A. and Storper, M. 2018. Regional inequality in Europe: evidence, theory and policy implications. *Journal of Economic Geography* 19:273-298.
- Jordan, N., Smith, B.P., Appleby, R.G., van Eeden, L.M. and Webster, H.S. 2020. Addressing inequality and intolerance in human-wildlife coexistence. *Conservation Biology* Online early doi: 10.1111/cobi.13471

- Kellert, S.R. 1996. *The Value of Life: Biological Diversity and Human Society*. Washington, DC: Island Press.
- Lê, S., Josse, J. and Husson, F. 2008. FactoMineR: An R Package for Multivariate Analysis. *Journal of Statistical Software* 25:1-18.
- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T. and Sand, H. 2011. Shoot shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society of London, Series B* 279:910-915.
- Linnell, J.D.C., Solberg, E.J., Brainerd, S., Liberg, O., Sand, H., Wabakken, P. and Kojola, I. 2003. Is the fear of wolves justified? A Fennoscandian perspective. *Acta Zoologica Lituanica* 13:27-33.
- Lopes-Fernandes, M., Soares, F., Frazão-Moreira, A. and Queiroz, A. 2016. Living with the beast: Wolves and humans through Portuguese literature. *Anthrozoos* 29:5-20.
- Macdonald, D.W. 2009. Lessons learnt and plans laid: Seven awkward questions for the future of reintroductions. In *Reintroduction of Top-Order Predators*, Eds. Hayward, M.W. and Somers, M.J., 411-449. Oxford: Blackwell.
- Mace, G. 2014. Whose conservation? *Science* 345:1558–1560.
- Madden, F. 2004. Creating coexistence between humans and wildlife: global perspectives on local efforts to address human-wildlife conflict. *Human Dimensions of Wildlife* 9:247–257.
- Mech, D.L. 2017. Where can wolves live and how can we live with them? *Biological Conservation* 210:310-317.
- Moretti, E. 2012. *The New Geography of Jobs*. Boston: Houghton Miffling Harcourt.
- Naturvårdsverket (2016) Nationell förvaltningsplan för varg. [National management plan for wolf] Stockholm: Naturvårdsverket. (In Swedish)
- Pedersen, S., Angelstam, P., Ferguson, M.A.D., Wabakken, P. and Storaas, T. 2019. Impacts of wolves on rural economies from recreational small game hunting. *European Journal of Wildlife Research* 65:87.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and R Core Team 2020. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-145, <https://CRAN.R-project.org/package=nlme>.
- Phillips, S.J., Anderson, R.P., Dudík, M., Shapire, R.P. and Blair, M.P. 2017. Opening the black box: an open-source release of Maxent. *Ecography* 40:887-903.
- Pohja-Mykrä, M. 2016. Felony or act of justice? Illegal killing of large carnivores as defiance of authorities. *Journal of Rural Studies* 44:46-54.
- Pooley, S., Barua, M., Beinart, W., Dickman, A., Holmes, G., Lorimer, J., Loveridge, A.J., Macdonald, D.W., Marvin, G., Redpath, S., Sillero-Zubiri, C., Zimmermann, A. and Milner-Gulland, E.J. 2016. An interdisciplinary review of current and future approaches to improving human-predator relations. *Conservation Biology* 31:513-523.
- Ray, J.C., Redford, K.H., Steneck, R.S. and Berger, J. (Eds.) 2005. *Large Carnivores and the Conservation of Biodiversity*. New York: Island Press.
- Røskoft, E., Händel, B., Bjerke, T. and Kaltenborn, B.P. 2007. Human attitudes towards large carnivores in Norway. *Wildlife Biology* 13: 172-185.
- Sandström, C., Johansson, M. and Sjölander-Lindqvist, A. 2015. The management of large carnivores in Sweden - challenges and opportunities. *Wildlife Biology* 21:120-121.
- Sjölander-Lindqvist, A. 2009. Social-natural landscapes reorganized: Swedish forest edge farmers and wolf recovery. *Conservation and Society* 7:130 —140.
- Skogen, K. and Kränge, O. 2020. The Political dimensions of illegal wolf hunting: Anti-elitism, lack of trust in institutions and acceptance of illegal wolf killing among Norwegian hunters. *Sociologia Ruralis* Online early doi: 10.1111/soru.12309

- Sollund, R. 2015. With or without a license to kill: Human-predator conflicts and theriocide in Norway. In *Environmental Crime and Social Conflict: Contemporary and Emerging Issues*, eds. Brisman, A., South, N. and White, R., 95-124. Farnham: Ashgate.
- Statistics Sweden, 2020. *Statistics Sweden Provides Society with Useful and Trusted Statistics*. Retrieved 4 August 2020 from <https://www.scb.se/en/>
- Stegmann McCallion, M. 2016. *Regionalism in Sweden*. Strasbourg: Assembly of European Regions.
- Treves, A. and Bruskotter, J. 2014. Tolerance for predatory wildlife. *Science* 344:476-477.
- Treves, A. and Karanth, K.U. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17:1491-1499.
- van Eeden, L.M., Crowther, M.S., Dickman, C.R., Macdonald, D.W., Ripple, W.J., Ritchie, E.G. and Newsome, T.M. 2017. Managing conflict between large carnivores and livestock. *Conservation Biology* 32:26-34.
- von Essen, E. and Allen, M.P. 2017. Reconsidering illegal hunting as a crime of dissent: Implication for justice and deliberative uptake. *Criminal Law and Philosophy* 11:213-228.
- von Essen, E. and Allen, M.P. 2000. 'Not the Wolf Itself': Distinguishing hunters' criticisms of wolves from procedures for making wolf management decisions. *Ethics, Policy & Environment* 23:97-113.
- Warton, D.I. and Hui, F.K.C. 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92: 3-10.

Table 1. Socioeconomic variables included in the analyses, as well as the correlation with and % contribution to the first two dimensions of a Principal Component Analyses describing socioeconomic condition of Swedish Municipalities. All characteristics were downloaded from a publicly available database managed by Statistics Sweden.

Variable	Years	Description	PCA Dim 1		PCA Dim 2	
			R	% Contr.	R	% Contr.
Population density	2000-2019	Number of inhabitants per square km, average 2000-2019	0.72	7.79 %	0.57	20.08 %
Population change	2000-2019	Average annual change in population size expressed as % of previous years population	0.81	9.75 %	0.42	10.84 %
Average age	2000-2019	Average age, both men and women	-0.76	8.70 %	-0.34	7.27 %
Life expectancy	2000-2019	Expected life span for a newborn in years, averaged across men and women	0.81	9.91 %	-0.11	0.85 %
Voting participation	2002-2018	Voting participation in governmental elections, average percentage participation of registered voters from 2002, 2006, 2010, 2014 and 2018 years elections.	0.76	8.65 %	-0.34	7.27 %
Median income	2000-2018	Average of the median annual income for men and women 20-65 years old	0.85	10.81 %	-0.10	0.65 %
Income change	2000-2018	Average annual change in income, expressed in percentage of previous years income	0.45	3.02 %	-0.61	23.38 %
Gini income index	2011-2018	Gini index calculated on all incomes	0.56	4.77 %	0.37	8.46 %
Low income standard	2011-2018	Percentage of population that has an annual income lower than the 60% quartile for the whole country	-0.83	10.50 %	0.35	7.60 %
Unemployment benefits	2014-2019	Number of whole year equivalents per 100 inhabitants 20-65 years of age that are funded completely by unemployment benefits	-0.56	4.63 %	0.38	9.17 %
Social benefits	2014-2019	Number of whole year equivalents per 100 inhabitants 20-65 years of age that are funded completely by social benefits other than unemployment	-0.87	11.23 %	0.18	1.80 %
University education	2000-2019	Percent of men and women 15-74 years old with a university education of at least 3 years	0.83	10.20 %	0.20	2.43 %

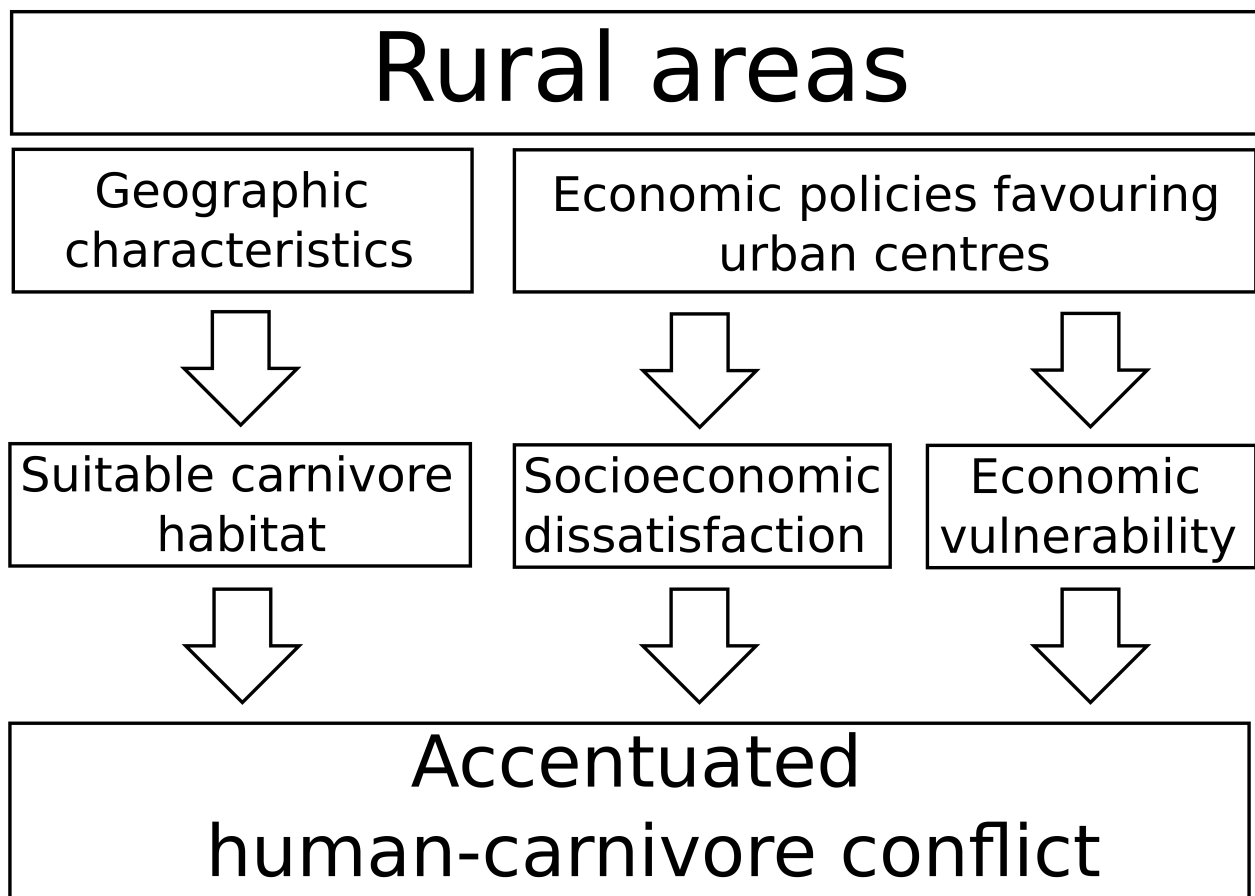


Fig 1. Conceptual model for how a geographic co-variation between habitat suitability for large carnivores and socioeconomic conditions may cause or accentuate existing human-carnivore conflicts in rural areas.

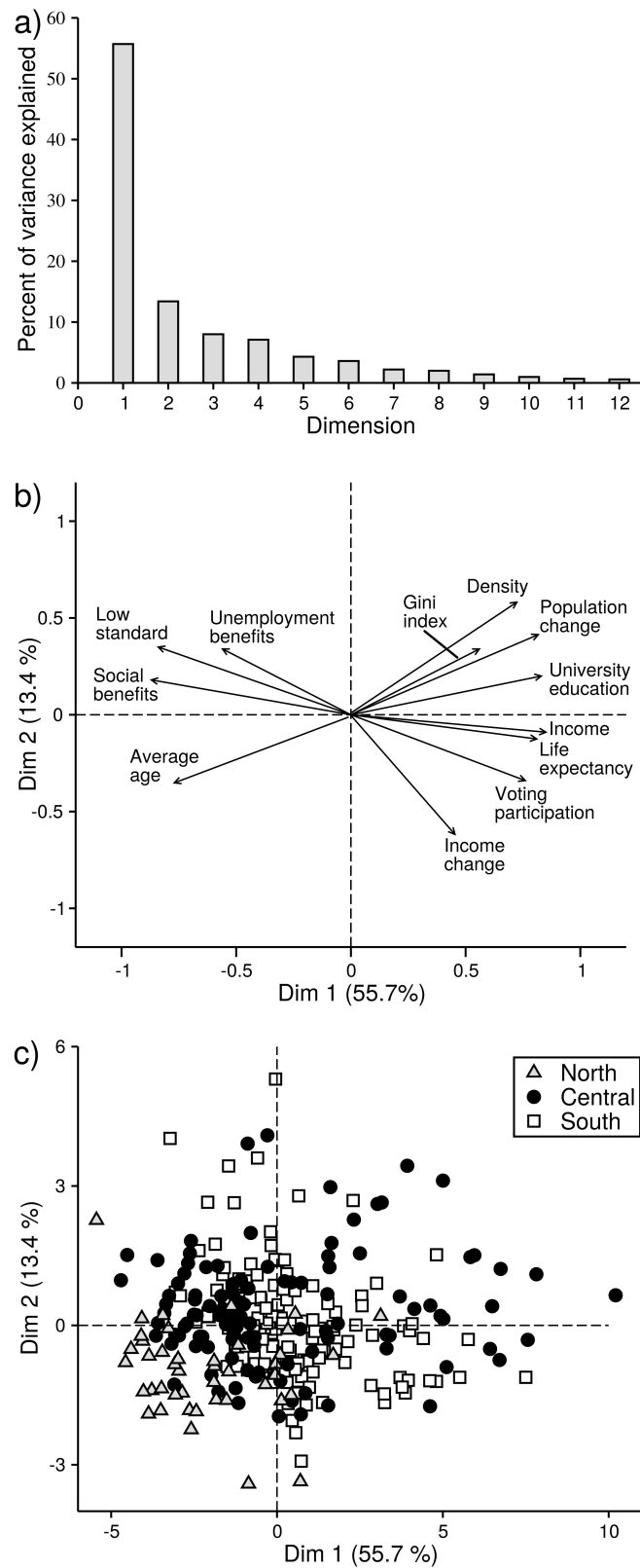


Fig 2. The variation in socioeconomic conditions between Swedish municipalities explained by each of the 12 dimensions of a Principal Component Analyses (PCA) (a), factor loadings of each of the socioeconomic variables onto the first two PCA dimensions (b), as well as the scores of the municipalities in the southern, central and northern management region for the first two PCA dimensions (c).

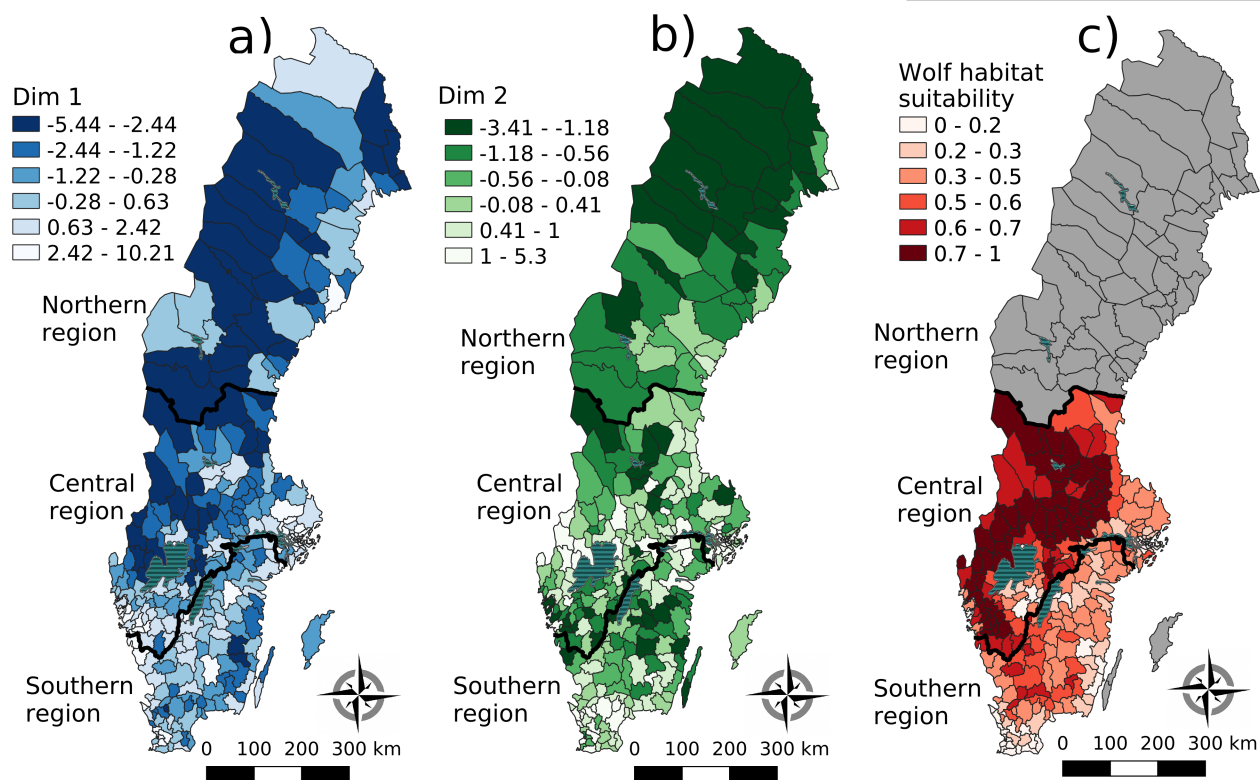


Fig 3. Spatial distribution of socioeconomic conditions quantified as the scores of the first (a) and second (b) PCA dimensions for all Sweden's municipalities, as well as the average wolf habitat suitability for all municipalities in the south and central management regions (c).

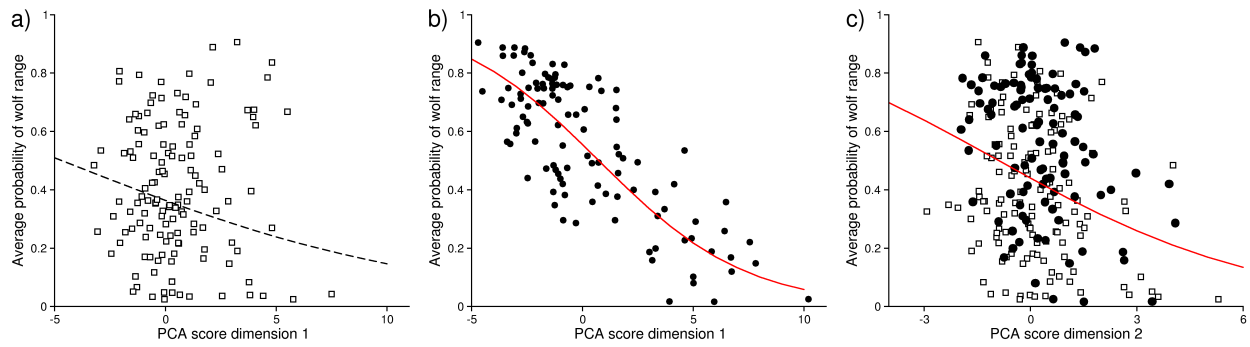


Fig 4. Relationships between the average wolf habitat suitability and socioeconomic conditions quantified as scores of the first PCA dimension for municipalities in the southern (a) and central (b) management regions, as well as relationships between the average wolf habitat suitability and socioeconomic conditions quantified as scores of the second PCA dimension for municipalities in both the southern and central management regions (c). Trend lines describe non-significant (dotted) and significant (solid) linear effects estimated on a logit scale.

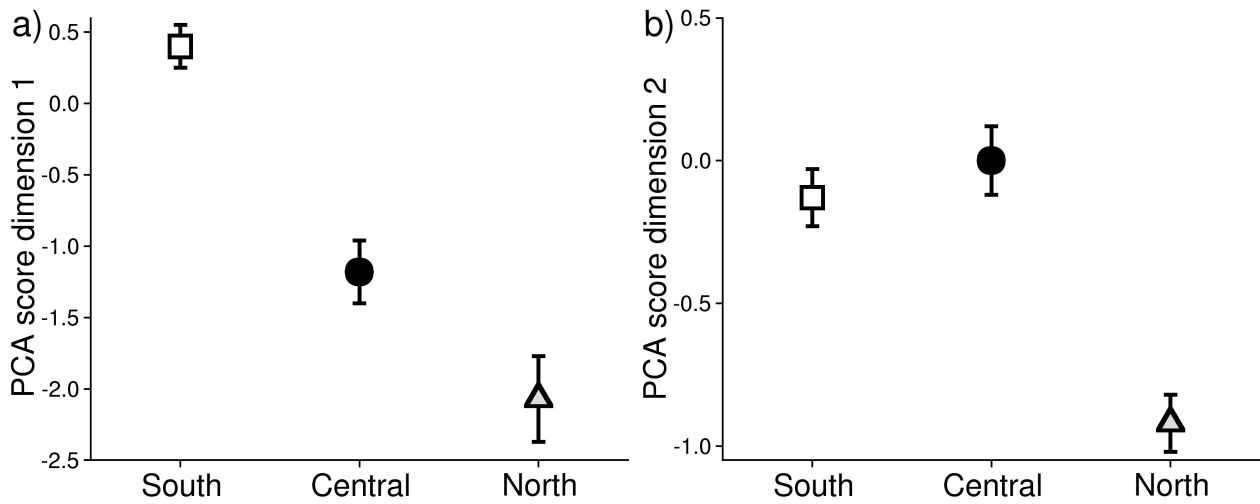


Fig 5. Socioeconomic conditions quantified as scores of the first (a) and second (b) PCA dimensions in areas previously identified as suitable for wolf range expansion, i.e. areas with suitable wolf habitat that lie outside of the current wolf distribution, within each of Sweden's three management regions. The figures present average and standard error of municipalities weighted by the number of cells within each municipality that were previously identified as range expansion areas.