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8 **Rule-based habitat suitability modelling for the reintroduction of the grey wolf**

9 **(*Canis lupus*) in Scotland**

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13 Vashti Gwynn[1*], Elias Symeonakis[1]

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18 [1]Department of Natural Sciences, Manchester Metropolitan University, Manchester, United

19 Kingdom

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23 *Corresponding author

24 Email: vashtigwynn@gmail.com (VG)

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Abstract

Though native to Scotland, the grey wolf (*Canis lupus)* was extirpated c.250 years ago as part of a global eradication drive. The global population has recently expanded, now occupying 67% of its former range. Evidence is growing that apex predators provide a range of ecological benefits, most stemming from the reduction of overgrazing by deer – something from which Scotland suffers. In this study, we build a rule-based habitat suitability model for wolves on the Scottish mainland. From existing literature, we identify the most important variables as land cover, prey density, road density and human density, and establish thresholds of suitability for each. Fuzzy membership functions are used to assign suitability values to each variable, followed by fuzzy overlay to combine all four: a novel approach to habitat suitability modelling for terrestrial mammals. Model sensitivity is tested for land cover and prey density, as these variables constitute a knowledge gap and an incomplete dataset, respectively. The Highlands and Grampian mountains emerge strongly and consistently as the most suitable areas, largely due to high negative covariance between prey density and road/human density. Sensitivity testing reveals the models are fairly robust to changes in prey density, but less robust to changes in the scoring of land cover, with the latter altering the distribution of land mainly through the 70 − 100% suitability range. However, in statistical significance tests, only the least and most generous versions of the model emerge as giving significantly different results. Depending on the version of the model, a contiguous area of between 10,139km^2 and 18,857km^2 is shown to be 80 to 100% suitable. This could be sufficient to support between 50 and 94 packs of four wolves, if the average pack range size is taken to be 200km^2. We conclude that in terms of habitat availability, reintroduction should be feasible.

Introduction

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49   The grey wolf (*Canis lupus*) is native to Scotland, but was extirpated by humans c.250 years

50   ago (1,2). This persecution was part of a global eradication effort that brought wolf numbers to their

51   lowest point between the 1930s and 1960s (3). However, due to subsequent legal protection and

52   conservation, the wolf population has expanded once again, and now occupies 67% of its former

53   global range, including substantial expansion in mainland Europe (4). It is, therefore, unnecessary to

54   re-establish wolf populations in the UK in order to conserve the species, but there is growing evidence

55   that the presence of native apex predators brings with it a range of ecological benefits (2,4,5). Ripple

56   et al. (4) showed that large carnivores are necessary to maintain biodiversity and ecosystem function,

57   and that their roles cannot be fully reproduced by humans, and Atkins et al. (5) state that the

58   elimination of large carnivores can suppress plant regeneration, due to population expansion and

59   behaviour changes in herbivores. Moreover, the grey wolf can cause mesopredator cascades

60   (affecting both mesopredators and their prey), and tri-trophic cascades (affecting every level of the

61   food-web down to plants) (4). Such benefits are needed in Scotland, where deer densities are beyond

62   ecological sustainability, and where red deer can reach a density of 150/km^2 in some areas in winter

63   (2,6). This has a serious impact on the structure, composition and function of Scottish ecosystems,

64   especially on tree regeneration, through overgrazing and over-browsing (2,6). The 1995

65   reintroduction of grey wolves into Yellowstone National Park is considered instructive as to what

66   may happen should wolves be reintroduced to the Scottish Highlands, as they share almost identical

67   key species (grey wolves, elk/red deer, aspen) (2). In Yellowstone, just a few wolves have had

68   profound effects, including tri-trophic cascades that ultimately improved river hydrology, and

69   increased abundance and diversity in many species (2).

70   Nilsen et al. (1) predict that if wolves were present in Scotland for 60 years, deer densities

71   would decline to 7/km^2, with >50% reduction in some places. This is in line with the Deer

72   Commission for Scotland's target of 6/km^2, and would greatly relieve the current financial burden of

73   annual hind culling in pursuit of this target (1). Additionally, it is proposed that the re-establishment

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74   of the "Landscape of Fear" would produce behavioural changes in deer, and thus ecosystem benefits,

75   beyond what reduction of numbers could achieve (2,7). Other benefits could include significant wolf-

76   related tourism and carbon sequestration due to regenerating woodland (1,4).

77   While wolf reintroduction in Britain is not currently being considered, the government's 25

78   Year Environment Plan sets out policy commitments to provide "opportunities for the reintroduction

79   of native species" (8). Reintroductions and rewilding are currently popular, and the reintroduction

80   of another keystone species – beavers – has received much attention and support. There is also

81   growing emphasis on the ecological importance of intact ecosystems, e.g. see Plumptre et al. (9). In

82   light of this, and the well-documented possible benefits of apex predators outlined above, the

83   feasibility and desirability of wolf reintroduction in the UK needs to be assessed. Manning et al. (2)

84   note the importance of a pre-existing body of research should reintroduction be considered in the

85   future. This study is limited to Scotland because it is the area of the UK likely to be most suitable,

86   due to its extensive deer-filled wild lands and low human density. Additionally, only the Scottish

87   mainland was considered, as this is where any reintroduction programme would likely take place.

88   Previous studies have explored some aspects of large predator reintroduction in Scotland, including

89   modelling hypothetical impacts of wolves on the deer population (1,10), and mapping habitat and

90   likely population expansion if lynx were reintroduced (11,12). Sandom et al. (10) take into account

91   some habitat elements in their model of a hypothetical large fenced Highland reserve containing

92   wolves. However – to our knowledge – no one has yet created a wolf habitat suitability model for all

93   of mainland Scotland.

94   There are many existing predictive habitat suitability models for wolves in countries where

95   they are already extant (notably in Italy, Switzerland, Poland, Germany and the northern USA) (13–

96   22). Usually, the environmental characteristics of the areas in which wolves are already present are

97   used to train the model (often a logistic regression model), which is then applied across the country

98   or region to identify other areas that may be suitable. The situation in Scotland is fundamentally

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99 different, as wolves are not currently extant there, and neither Italy, Switzerland, Poland, Germany

100 nor the northern USA can be considered sufficiently similar to Scotland, as regards land cover,

101 climate and elevation, to be able to apply their habitat selection models directly. Fuzzy logic

102 analysis is widely used in predictive modelling, including marine and aquatic habitat suitability

103 modelling (23–26). It recognises marginal locations that sit on the boundaries of classes by assigning

104 *likelihood* of class membership to each location (23,27)However, with the exception of the study by

105 Zabihi Afratakhti et al. (27) fuzzy logic analysis is notably absent from the field of terrestrial habitat

106 suitability modelling. Thus its use in this study represents a novel approach to mammalian habitat

107 suitability modelling.

108 Here, we assess habitat suitability for wolves in mainland Scotland employing a rules-based

109 approach, based on existing knowledge about wolf ecology (23), and fuzzy logic analysis, which

110 allows for dataset inaccuracies and uncertainty in both the definition of attribute classes and in the

111 measurement of the phenomenon. We carry out a sensitivity analysis of the model for the variable

112 whose suitability is most uncertain (land cover), and for the variable for which we have the least data

113 (prey density). Along with the use of fuzzy logic analysis, this allows for the incorporation of

114 uncertainty in modelling and subsequent decision-making (28). This is particularly important in

115 habitat suitability studies, as they contain numerous possible sources of error and/or uncertainty, e.g.

116 spatial data inaccuracies, definition of rules based on other environments, etc (28,29).

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Methods

Study Area

120 Scotland is a north-west European nation of 78,352km^2, occupying the northern third of the

121 island of Great Britain (Fig 1) (30,31). It has a temperate oceanic climate, that is wetter in the west

122 with milder winters. Mean temperature in the coldest month is approximately 4ºC, and in the warmest

123 month, 14ºC. Annual precipitation ranges from 635mm - >1000mm east to west, and significant

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124 snow falls on land above 460m in the winter (30). Glaciated in the Pleistocene, the Highlands in the

125 north are mountainous and rugged, whereas the Central Lowlands are relatively flat, and the Southern

126 Uplands are hilly (31). Almost all of Scotland's primary forests have been cleared, and peatlands are

127 widespread on the moors and hills, which are largely used for sheep farming and deer and grouse

128 estates (30,31). Only 10% of the UK's population live in Scotland, 75% of which dwell in the Central

129 Lowlands, leaving rural areas sparsely populated (30).

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Fig 1: Physical map of Scotland and its location within north-west Europe inset. The mountains of the Highlands/Grampians in the North, the belt of the Central Lowlands, and the hills of the Southern Uplands can be clearly seen (Ordnance Survey, 2013; OpenStreetMap, n.d.).

Rationale

132 Wolf habitat must be considered at a landscape scale, due to the size of the pack territories,

133 which are typically $100 - 200\text{km}^2$, but vary greatly (13,17,32), and due to wolves' long-distance

134 dispersal, which can be hundreds of kilometres (32). Many European studies find there is a strong

135 correlation between wolf presence and forest cover (14,15,19,20), but it must also be recognised that

136 in these countries, areas with *low* human influence and *high* prey density tend to have correspondingly

137 *high* forest cover. For instance, the Swiss Valais is 22% forest, and nearly all ungulates are restricted

138 to forest habitats, especially in winter (18). Jędrzejewski et al. (19,20) also attribute Polish wolf pack

139 preference for forest cover to avoidance of humans. This association between high forest cover and

140 high prey density/low human presence is not the case in Scotland, which is only 18.5% forest (mostly

141 conifer plantations) and where heathland and upland bog constitute the majority of its unpeopled and

142 deer-stocked wild lands (33). Meanwhile, many American models find that wolf presence and

143 abundance is more directly related to prey density or human-caused mortality risk than land cover

144 (13,16,21). For instance, the wolf packs in the Canadian Arctic follow the caribou herds regardless

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145   of habitat (34). Similarly in north-eastern USA, prey availability and not habitat type explained 72%

146   of spatial wolf population variation (16).   Road density is also recognised as a crucial factor in habitat

147   suitability in multiple studies (e.g. (35,36)). This difference between American and European studies

148   suggests that either different limiting factors are at play, or that high covariance makes it hard to

149   disentangle the importance of each variable.

150   Similarly, slightly different wolf predation behaviours emerge from different European

151   studies, though wild ungulates always predominate (though see Ciucci et al. (14), for scavenging

152   behaviour on garbage dumps) (32,37). Though roe and red deer form the majority of wolf diets in

153   most European studies, some studies suggest red deer are preferred (though roe deer often still make

154   up the majority of the diet due to higher availability) (19,38–42). Therefore, it is likely that in

155   Scotland, both roe and red deer would be predated, though there may be a preference for red deer

156   where they are available. Fallow and Sika deer are also found in Scotland, but little data exists for

157   wolf predation on these species (43).

158   Despite these variations across studies, land cover, prey density, road density and human

159   density emerge as the most important factors in wolf habitat suitability. As regards land cover, we

160   noted which cover types are associated with wolf presence and absence, but as regards the other three

161   variables – which are continuous rather than categorical variables – we needed to establish thresholds

162   of suitability and unsuitability.

163   Prey densities that characterise areas of wolf presence (i.e. suitable habitat) vary across studies.

164   Jędrzejewski et al. (20) noted a drop-off in wolf presence only when prey densities were as low as

165   0.6 deer/km^2, but other studies find density requirements of at least 4/km^2, with up to 13 elk per km^2

166   recorded in the wolf ranges in Yellowstone National Park (10,21,22,37,44).

167   As regards roads, road density (km/km^2) is the standard metric used in studies that assess wolf

168   responses to roads (13,16,18–20,35,36). Recorded road densities in areas of wolf presence (i.e.

169   suitable habitat) vary from 0.2km/km^2 to around 0.4 or 0.5km/km^2. Though there are areas with road

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170   densities of 0.7km/km^2 being resettled by wolves, most studies thus far find such densities to be

171   largely unsuitable (13,16,18,35,36,45).

172   Recorded human densities in areas of wolf presence (i.e. suitable habitat) begin at 0.43/km^2

173   (21), but there is some variation in where the upper limit lies, with the same study finding an average

174   of just 2.33 people/km^2 in non-pack areas, whereas other studies record human densities all the way

175   up to 36.7/km^2, especially in Europe (13,18,22,45–47).

176   Given these varying preferences and behaviours in different regions (none of which are

177   entirely comparable to Scotland), it may seem challenging to derive suitability rules that would apply

178   to Scotland. However, the wolf's generalist ecology helps to offset this. Wolves are not habitat

179   specific, and nor are they necessarily wilderness species. They have colonised habitats throughout

180   the northern hemisphere wherever they are protected from persecution, from 20° north up to the Arctic

181   (3,13,48). Wolf core ranges have been found to include a wide range of habitats in addition to forests,

182   including pasture, chaparral, eskers, heath tundra, and human garbage dumps (14,34,49). Recently

183   wolves successfully recolonised a National Park in the Netherlands, an urbanised country with an

184   average human population density of 512/km^2 (against Scotland's 70/km^2) (50,51). Additionally,

185   Scotland was until recently (ecologically speaking) part of the wolf's range, and it was eradicated by

186   persecution rather than by a lack of suitable habitat. Of course it may be fallacious to assume that

187   because Scotland offered suitable wolf habitat in the past, it continues to do so now and in the future,

188   but this only increases the need for rigorous study to test if that is so (29). Osborne and Seddon (29)

189   recognise that it is essential to model extensively before reintroduction of any species, and that

190   unsuitable habitat may be the main reason for reintroduction failures in the past.

191   Once the most important factors had been identified, and suitability thresholds established for

192   each, fuzzy membership was applied to GIS datasets of the three continuous variables across the

193   Scottish mainland, while land cover types were allocated scores and likewise mapped. The resulting

194   output maps were combined using fuzzy overlay (Fig 2). This process was applied to six variations

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195 in input data, to explore uncertainty and to test sensitivity. The result is a set of six output maps, each

196 containing all four variables, grading the Scottish mainland according to its suitability as wolf habitat.

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Fig 2: Flowchart of process. A summary of the analysis process, from input datasets to output maps. Note there are output maps for each variable individually, and then further output maps of all four variables combined using fuzzy overlay.

Datasets 198

199 Spatial datasets for the four variables for Scotland were assembled in a GIS (ArcGIS Desktop

200 10.7.1 (52)), clipped to the Scottish mainland and converted to raster if originally in vector format

201 (Table 1).

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203 **Table 1. Datasets and their sources used in the analysis of habitat suitability.**

Variable	Source	Date of data collection/ dataset creation
Land cover	Corine Land Cover vector map, 2020 version https://land.copernicus.eu/pan-european/corine-land-cover/clc2018?tab=mapview	2018
Prey density	Scottish Natural Heritage Deer Count Density vector map, revised 2018 https://gateway.snh.gov.uk/natural-spaces/dataset.jsp?dsid=DCD	2010
Road density	Ordnance Survey's Open Roads vector map https://www.ordnancesurvey.co.uk/business-government/products/open-map-roads	2020
Human density	National Records of Scotland (2011). 2011 Census: boundary data vector map https://beta.ukdataservice.ac.uk/datacatalogue/studies/study?id=5819&t	2011

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ype=Data%20catalogue	

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Land Cover

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208   The Corine Land Cover map is a European land cover inventory in 44 classes, based on

209   Sentinel and Landsat imagery. It is classified at three levels of increasing thematic detail (e.g. the

210   land cover type "Wetlands" is subclassified into "Coastal Wetlands" and "Inland Wetlands", which

211   are themselves subclassified into five further classes). The middle level of classification was used,

212   as it had an appropriate level of thematic resolution. Each land cover type was scored for wolf

213   suitability according to the available literature on wolf habitat preferences described in the Rationale

214   (Table 2). A similar approach was used by Sandom et al. (10) in their modelling of a hypothetical

215   fenced reserve in Scotland, but here an index between 0 and 1 was used, as that is comparable to the

216   way fuzzy membership is allocated (where 0 indicates unsuitable habitat, and 1 suitable habitat).

217

218   **Table 2. Land cover suitability scores.**

Land cover	Score
Arable land	0
Artificial, non-agricultural areas	0
Coastal wetlands	0.4
Forest	1
Heterogeneous agricultural areas	0.2
Industrial, commercial and transport units	0
Inland waters	0
Inland wetlands	0.2, 0.4 & 0.6[a]
Marine waters	0

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Mine, dump and construction sites	0
Open spaces with little or no vegetation	0.2, 0.4 & 0.6[a]
Pastures	0
Permanent crops	0
Shrub and/or herbaceous vegetation associations	0.2, 0.4 & 0.6[a]
Urban fabric	0

219   [a]*These land cover types were scored three times due to uncertainty about their level of suitability.*

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221   The suitability of the land cover types "Inland wetlands", "Open spaces with little or no

222   vegetation", and "Shrub and/or herbaceous vegetation associations" was particularly hard to score,

223   because these land cover types are uncommon in areas where other wolf habitat suitability studies

224   have been performed, and thus their suitability is unclear. Their level of suitability is also crucial as

225   they are dominant habitats in Scotland. Therefore, the model was run once with them scored at 0.2,

226   once at 0.4, and once at 0.6, so that the model sensitivity to this particular variable could be explored.

227   These scores can be considered to indicate substantially unsuitable, somewhat unsuitable and

228   somewhat suitable habitat, respectively.

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230   **Prey Density**

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232   The map of deer density had a resolution of 1km^2, with count data attached to each 1km^2 cell.

233   Due to the herding behaviour of red deer in the Highlands, deer density was highly aggregated, i.e.

234   one cell could contain dozens of deer while those around it contained none, reflecting where the herd

235   happened to be on the day of the count. As this snapshot did not accurately reflect the realised spatial

236   density of deer over time, kernel density estimation (KDE) was applied to each herd location, with

237   an output cell size of 50m and a search radius of 1480m (representing the average home range of a

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238   red deer) (53,54). This "smooths" the density over a wider area, in recognition of the fact that the

239   herd will move around its range, and so the entire range may be considered to offer prey (55).

240   Data from multiple studies suggest roe deer are an important component in wolf diets (see

241   Rationale). Unfortunately, almost no roe deer are included in SNH's Deer Count Density map, and

242   no alternative roe deer density data was found. However, Campbell is cited as stating that roe deer

243   density in the Highlands is 7.4/km^2 and in the Southern Uplands 5.5/km^2 (43). Therefore analysis was

244   performed once with only the SNH dataset, and then a second time in which roe deer were additionally

245   incorporated. They were incorporated at the densities mentioned above in every km^2 cell for the

246   Highlands and Southern Uplands (in the council areas of Highland, Dumfries and Galloway, and

247   Scottish Borders, to be precise). Higher deer density suitability thresholds were used in the second

248   version to account for the smaller body size of roe deer. The values used were, as with the red deer,

249   guided by existing literature on roe deer densities in wolf territories (22). Due to the paucity of roe

250   deer density data, this should be considered only as indicative of whether roe deer presence/absence

251   might strongly change the outcome of the model, and more research is no doubt needed.

252

253   **Road Density**

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255   Road density (km/km^2) was calculated from the Open Roads vector map at a resolution of

256   0.5km^2. No weighting was applied to roads of different rank, as this does not seem to be common

257   practice in wolf/road studies, but this could be worthy of further investigation.

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259   **Human Density**

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261   Human density (people/km^2) was calculated from the boundary census data vector map and

262   converted to raster. With population data available only at census boundary scale, this is the dataset

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263   with the coarsest resolution. These boundaries are small in urban areas, where the population is high,

264   but large in rural areas.

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266   **Processing**

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268   Thresholds that represented completely suitable conditions (scored as 1) and completely

269   unsuitable conditions (scored as 0) were established from the literature as regards deer, road and

270   human densities (Table 3). Fuzzy membership with a linear membership type was then applied to

271   each of these datasets accordingly, resulting in maps showing the suitability of that variable for

272   wolves across mainland Scotland. This process was repeated for the deer density dataset with

273   additional roe deer densities incorporated. The land cover dataset could not be processed using this

274   method, because although the suitability scoring applied is numeric, it is categorical rather than

275   continuous data, and therefore has no marginal cases (27).

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279   **Table 3. Thresholds of suitability.**

Variable	Suitable	Unsuitable
Prey density without roe deer	$\geq 5.5/km^2$	$\leq 1/km^2$
Prey density with roe deer	$\geq 7/km^2$	$\leq 3/km^2$
Road density	$\leq 0.23 km/km^2$	$> 0.7 km/km^2$
Human density	$\leq 2/km^2$	$\geq 37/km^2$

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281   All four outputs were then assembled using fuzzy overlay with overlay type gamma of 0.9.

282   Due to the paucity of fuzzy analysis in habitat suitability studies, there was no justification for using

283   a different value, but this could be investigated further. Because of the two versions of deer density

     13

284 and three versions of land cover datasets in use, this resulted in six output maps. These maps each

285 incorporate all four variables, but with some changes in input values in the deer density and land

286 cover variables (Table 4).

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288 **Table 4. Versions of land cover dataset and prey density dataset used in each model.**

	Inland wetlands, Open spaces with little or no vegetation, and Shrub and/or herbaceous vegetation		
	Suitability score = 0.2	Suitability score = 0.4	Suitability score = 0.6
Without roe deer	Model 1 (Fig 3a)	Model 2	Model 3 (Fig 3b)
With roe deer	Model 4 (Fig 3c)	Model 5	Model 6 (Fig 3d)

289

290   The fuzzy overlay maps were reclassified into 10 equal classes of suitability using ArcMap's

291 Reclassify tool. The distribution of pixels across the classes could then be used to calculate area and

292 proportion of the Scottish mainland falling into each class, i.e. what proportion of land is 0-10%

293 suitable, 10-20% suitable, and so on. Finally the Create Random Points tool and the Sample tool

294 (resampling technique: nearest) were used to extract cell values from the same 500 randomly-

295 generated points on each of the 6 fuzzy overlays, and a test for difference was performed in SPSS.

296 As the data was strongly non-normal (Shapiro-Wilk: p=<0.001), Kruskal-Wallis with all pairwise

297 comparisons was used.

298

299 # Results

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301   Fig 3 shows the maps resulting from fuzzy membership analysis on land cover (Fig 3a, 3b,

302   3c), prey density (Fig 3d and 3e), road density (Fig 3f) and human density (Fig 3g). Land cover and

303   prey density have three and two variations respectively, as per Table 4.

304

Fig 3: Fuzzy membership output maps. These show the suitability of the four variables: land cover

(a,b,c) with three key types scored at 0.2, 0.4 and 0.6 respectively; prey density (d,e) without and with

roe deer incorporated as a baseline density in two areas; road density (f) and human density (g). The

Highlands and Grampians emerge consistently as the most suitable areas in all variables.

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306   Fig 3a, 3b and 3c make explicit the large areas of Scotland covered by the three land cover

307   types on which there is little suitability data: Inland wetlands, Open spaces with little or no vegetation,

308   and Shrub and/or herbaceous vegetation associations. Meanwhile, it can be seen that red deer

309   densities are largely suitable in the Highlands and Grampians (Fig 3d and 3e). The addition of a roe

310   deer baseline density in three council areas increases the suitability of the Highlands and Southern

311   Uplands. Human density (Fig 3g) is suitable for wolves across a large proportion of Scotland, but

312   suitable road densities (Fig 3f) are far more limited, again to the Highlands and Grampians.

313   Fig 4 shows four of the six fuzzy overlay habitat suitability maps, each combining the four

314   variables as per Table 4. Fig 4a and 4b do not include a roe deer baseline density along with red deer

315   density, and Fig 4a and 4c score the three key land cover types at 0.2, whereas Fig 4b and 4d score

316   them at 0.6. The two fuzzy overlay maps using the three land cover types scored at 0.4 can be seen

317   in the Supporting Information (S1 Fig). The more suitable habitat is concentrated in the Highlands

318   and Grampian Mountains in all model outputs.

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Fig 4: Overall wolf habitat suitability. Fig 4a corresponds to Model 1, Fig 4b to Model 3, Fig 4c to

Model 4 and Fig 4d to Model 6 (Table 4).

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320   The area and proportion of mainland Scotland falling into each of ten equal classes of

321   suitability was calculated for each model (Table 5). This underlines the fact that the majority of

322   Scotland is unsuitable according to these models, and that this does not vary much between models.

323   There is more variation at the high suitability end of the scale, with between 0.6% and 21% of the

324   area (or between 384km^2 and 14259.5km^2) rated most suitable (0.9 – 1.0), depending on the model

325   used. Regardless of the model used, land is concentrated at either end of the scale of suitability, with

326   very little semi-suitable habitat.

327

328   **Table 5. Proportion of Scotland by suitability class.**

Suitability		Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
0.0 - 0.1	Area (km^2)	51980.5	51981.5	51980.0	47305.5	47305.5	47306.0
	Proportion	76.5	76.5	76.5	69.7	69.7	69.7
0.1 – 0.2	Area (km^2)	0.0	0.0	0.0	0.0	0.0	0.0
	Proportion	0.0	0.0	0.0	0.0	0.0	0.0
0.2 – 0.3	Area (km^2)	1.0	0.5	0.5	0.0	0.0	0.0
	Proportion	0.0	0.0	0.0	0.0	0.0	0.0
0.3 – 0.4	Area (km^2)	15.5	12.0	6.5	9.5	5.5	4.0
	Proportion	0.0	0.0	0.0	0.0	0.0	0.0
0.4 – 0.5	Area (km^2)	86.5	46.0	37.0	58.0	30.0	20.0
	Proportion	0.1	0.1	0.1	0.1	0.0	0.0
0.5 – 0.6	Area (km^2)	346.0	200.0	146.0	225.0	139.5	101.0
	Proportion	0.5	0.3	0.2	0.3	0.2	0.1
0.6 – 0.7	Area (km^2)	1244.0	691.5	492.0	953.0	503.5	351.5
	Proportion	1.8	1.0	0.7	1.4	0.7	0.5

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0.7 – 0.8	Area (km²)	4097.5	2114.0	1492.0	4131.5	1917.5	1270.5
	Proportion	6.0	3.1	2.2	6.1	2.8	1.9
0.8 – 0.9	Area (km²)	9755.5	7076.0	4237.0	14477.5	8820.5	4597.0
	Proportion	14.4	10.4	6.2	21.3	13.0	6.8
0.9 – 1.0	Area (km²)	384.0	5791.5	9519.0	750.0	9190.0	14259.5
	Proportion	0.6	8.5	14.0	1.1	13.5	21.0

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330   Plotting this in graph form makes it plain that the different models have little impact on the

331 distribution of land within the less suitable categories, but a larger impact on distribution in the more

332 suitable categories (Fig 5 – note the logarithmic scale on the y-axis). It also becomes evident that the

333 changes in land cover scoring have more of an impact on results than the addition of roe deer baseline

334 densities.

335

Fig 5: Area of Scotland by suitability class. Area of the Scottish mainland that falls into each of ten classes of suitability under different models (models 1 - 6 from left to right). Note that the Y-axis uses a logarithmic scale. All models show a similar pattern, with the distribution being highly uneven, and most areas being either completely unsuitable or substantially/completely suitable.

336   Testing for difference in a sample of 500 randomly-generated cell values taken at the same

337 points for all six fuzzy overlay maps shows that there is only a significant difference in results

338 between Model 1 and Model 6, i.e. the most and least "generous" models (H = -3.47, df = 5, p =

339 0.008, using the adjusted significance value).

340

341

342 **Discussion**

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344   Our results have shown that there is a high level of covariance between three of the variables,

345   with the most suitable areas in terms of prey density, road density and human density all concentrated

346   in the same regions (Fig 3). This results in the Highlands and Grampian mountains emerging strongly

347   and consistently in Fig 4 as the areas most suitable for wolves in mainland Scotland. Though this

348   area is contiguous, it is bisected by the A82 and the many lochs of the Great Glen, which could be

349   barriers to wolf movement. Human density, prey density and road density are suitable throughout

350   this region, and the addition of roe deer to the prey density map makes little difference. This is partly

351   because in the Highlands the high densities of red deer already reach the suitability threshold, whereas

352   in the Southern Uplands, the majority of the region is excluded anyway due to high road densities. It

353   is also partly because the adjustment of the suitability thresholds upwards to account for the smaller

354   body size of roe deer (Table 3) somewhat negates the gains of including them.

355   However, the suitability of the fourth variable, i.e., land cover, depends heavily on how

356   suitable open heath and bog habitat is for wolves. It is the scoring of three land cover types in this

357   variable that make the largest difference in the fuzzy overlay maps. Though in all cases the Highlands

358   and Grampians still emerge as most suitable, differences in scoring mean they may be anywhere

359   between somewhat suitable and completely suitable (between 0.7 and 1.0).

360   In terms of sensitivity, it can thus be concluded that the model is not particularly sensitive to

361   the changes in prey density used here. However, it is somewhat sensitive to changes in land cover

362   scoring: though the regions with highest suitability do not change, their level of suitability does.

363   As regards prey density, road density, and human density, the models could be considered

364   relatively conservative. This is due to two reasons: the estimates of suitability and unsuitability

365   adopted as thresholds were conservative; and prey density is likely to be higher and more widespread

366   than the SNH's deer counts suggest, as these counts mostly only include red deer spotted in open

367   areas where and when a count is carried out. The British Deer Society's distribution survey (56) finds

18

368   that red deer are extant also in the Southern Uplands (which is not represented in the SNH counts),

369   roe deer are common across Scotland, and fallow and sika deer are also found patchily in the

370   Cairngorms, Highlands, west Scotland and the central Southern Uplands. However, it must be noted

371   that regardless of prey density much of Scotland would remain unsuitable for wolves due to high road

372   densities (Fig 3f).

373   Deer densities far exceed the threshold of suitability in much of the Highlands and Grampians

374   with many areas holding $>35/km^2$ according to SNH's deer counts (after KDE processing).

375   Hetherington and Gorman (43) quote an average density of 12.2 deer of all species/km^2 in the

376   Highlands, while $11–12/km^2$ is estimated by Sandom et al. (10). This is significant because wolf pack

377   range size is largely determined by prey availability (16,32,37). Recorded range sizes vary from

378    $33km^2$ to $6272km^2$ but average $100 – 200km^2$ (13,17,32,45). Fuller (37) found that at a density of

379   6.2 white-tailed deer per km^2 (roughly half the Highland deer density) pack range size was only

380    $116km^2$. Meanwhile, Sandom et al.'s (10) modelling suggested that a Highland fenced reserve of

381    $600km^2$ would sustain 2 packs of 4 wolves for at least 100 years. At their most conservative, the

382   models used in this study place an area of $10,139km^2$ between 80% and 100% suitable, and at their

383   most generous, $18,857km^2$ is $80 – 100\%$ suitable. This suggests that there may be sufficient wolf-

384   suitable area to support between 50 and 94 packs of 4 wolves, if pack territory size is taken to be

385    $200km^2$. However, it should be noted that the minimum size required for a single pack is unclear due

386   to variations in range size recorded in the literature, and Sandom et al. (10) found that a fenced reserve

387   of $200km^2$ was too small to support a Highland wolf pack for 100 years (though fencing brings with

388   it implications that an unfenced population would not face). Additionally, a single – or even several

389   – packs is not a self-sustaining population, as evidenced by the isolated wolf population on $544km^2$

390   Isle Royale in Lake Superior, whose numbers dwindled from 50 in 1980 to 2 in 2016 before

391   reintroductions bolstered them (57). Indeed in 1992, the US Fish and Wildlife Service stated that an

392   area of $25,000km^2$ was required for a self-sustaining wolf population (16).

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393   However, the evidence base of what wolves require is still developing. Linnell et al. (48),

394   Mech (3), and Mladenoff et al. (13) all note that with protection from persecution, wolves are

395   recolonising areas previously thought unsuitable due to high human and road densities. Future

396   observations of recolonising wolves in Europe are likely to be instructive as to what wolves prefer

397   and tolerate. Clarification on wolf preferences as regards open upland habitats is particularly needed

398   for assessment of Scottish habitat suitability, as studies currently conflict on how essential forests are

399   for wolves (see Rationale). Though this is the largest data gap as regards modelling Scottish habitat

400   suitability, other areas of future research could also include wolf response to roads. The standard in

401   wolf habitat studies is employing a road density measure of km/km^2. However, Jędrzejewski et al.

402   (20) found that Polish wolves avoided a 250m wide belt along roads, so the use of buffer zones in

403   models may be more beneficial. Additionally, there seems to be little research on the implications of

404   roads of different class, and this could be explored further. Further research into Scottish habitat

405   suitability would also benefit from more comprehensive deer density datasets, or else modelling of

406   deer populations across Scotland that is more sophisticated than the KDE smoothing used here.

407   Reinecke et al. (55) point out that one of the weaknesses of KDE is that it includes invalid areas (for

408   instance a loch), and suggest minimum convex polygons or α-local convex hulls as alternative

409   methods for modelling red deer. Dasymetric interpolation may also provide a more realistic model

410   of deer densities (58). However, as our sensitivity testing indicated that changes in deer density did

411   not particularly affect the model output, we did not refine our processing for this study.

412   There are many considerations regarding the return of wolves to Scotland that are beyond the

413   scope of this study. These include the requirements of maintaining wolf genetic diversity and

414   metapopulation, which would require either an area far bigger than that needed to support a few packs,

415   or else regular introductions of additional animals. There are also implications arising from wolf

416   dispersal (which can be many hundreds of kilometres) and social ecology (which is complex and

417   could be negatively affected in a small, constrained population) (32). These implications are not

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418 explored here, but would be worth further study. While this study finds deer densities are easily

419 sufficient to support wolves in the Highlands and Grampians, it does not model the long-term

420 predator-prey relationship or the likely impact on deer population dynamics. Lastly, one of the most

421 important considerations in any reintroduction project is public attitude and impacts on local

422 communities. With apex predators there is a particular risk of human-wildlife conflict, especially due

423 to livestock predation. Wolf reintroduction also has the potential to affect the recreational value of

424 Scotland's wild lands, and even its Protected Areas. See Sandom et al. (10) for modelling of predator-

425 prey and population dynamics of wolves in the Highlands, and for discussion of the implications for

426 recreation and Protected Areas. See Nilsen et al. (1) for modelling of predator-prey dynamics and

427 ecological impacts should wolves be released in Scotland, and discussion of public attitudes and

428 perceptions.

429 With the recolonisation of Europe by wolves, Britain increasingly becomes an outlier in its

430 lack of apex predators. If the nation were not an island, wolves would likely soon cross our borders,

431 if they had not already done so. As it is, short of escape from captivity, it is impossible for wolves to

432 recolonise naturally, regardless of the suitability of our habitats or the desirability of their presence.

433 Whether they return to Britain is a decision we must make actively, and in full consideration of the

434 wolf's requirements and impacts. Therefore conservationists need to anticipate evidence needs now

435 (2). As well as the need to fill knowledge gaps (some of which are identified above) both Manning

436 et al. (2) and Sandom et al. (10) advocate reintroduction experiments in large-scale Highland

437 enclosures, which would allow us to discover the impacts of wolves on deer and ecosystems in general,

438 in the context of the Highlands. This study supports previous conclusions that in terms of habitat

439 suitability, the Highlands or Grampians would be the most appropriate places for wolf reintroduction.

440 We recommend further research into the knowledge gaps outlined, and beyond that – should Scotland

441 still appear suitable for wolves, as we find – consideration be made of the desirability of

442 reintroduction.

21

443

Conclusion

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446   This study set out to identify the level of habitat suitability for wolves in the Scottish mainland. We have established thresholds of suitability and unsuitability from the literature as regards the four most important habitat variables: land cover, prey density, road density and human density. We mapped each variable according to its suitability across mainland Scotland using fuzzy membership analysis, and then combined all the variables into maps of overall suitability using fuzzy overlay. The Highlands and the Grampians emerged strongly as the most suitable areas, and sensitivity testing showed the model was fairly robust to changes in the prey density inputs, but less robust to changes in the land cover inputs, which we identify as an area in need of further research. Between 10,139km^2 and 18,857km^2 are found to be 80 – 100% suitable, depending on the model used, which may be sufficient to support between 50 and 94 packs of 4 wolves.

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8. Supporting information

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S1 Fig: Habitat suitability maps produced using the three land cover types scored at 0.4. *These were produced by Model 2 (a) and Model 5 (b) in Table 4, respectively.*
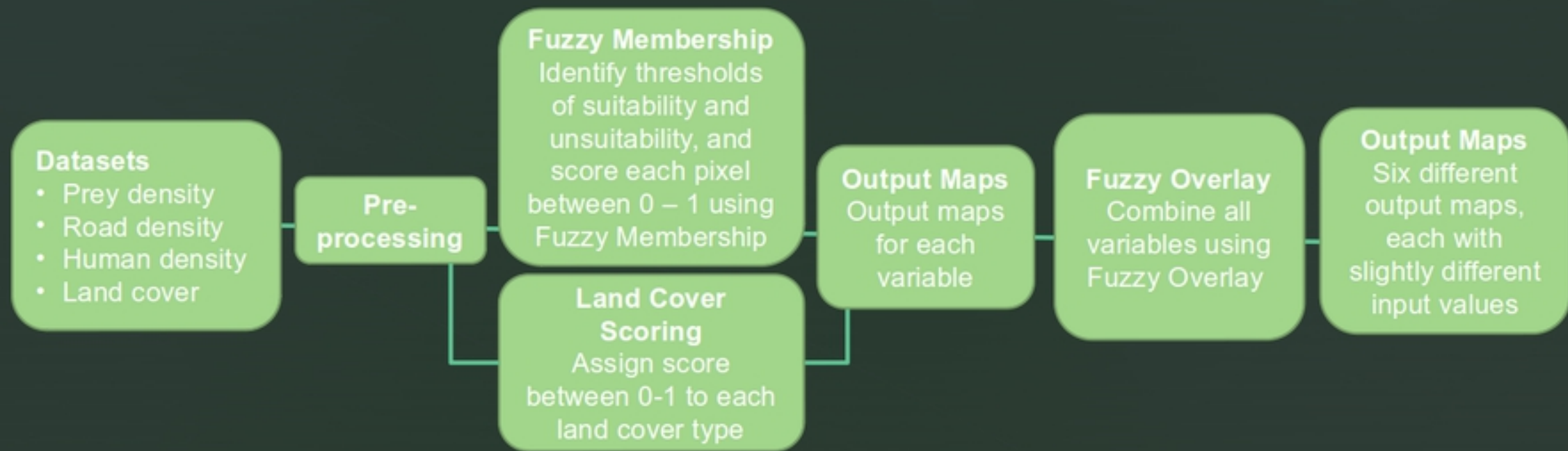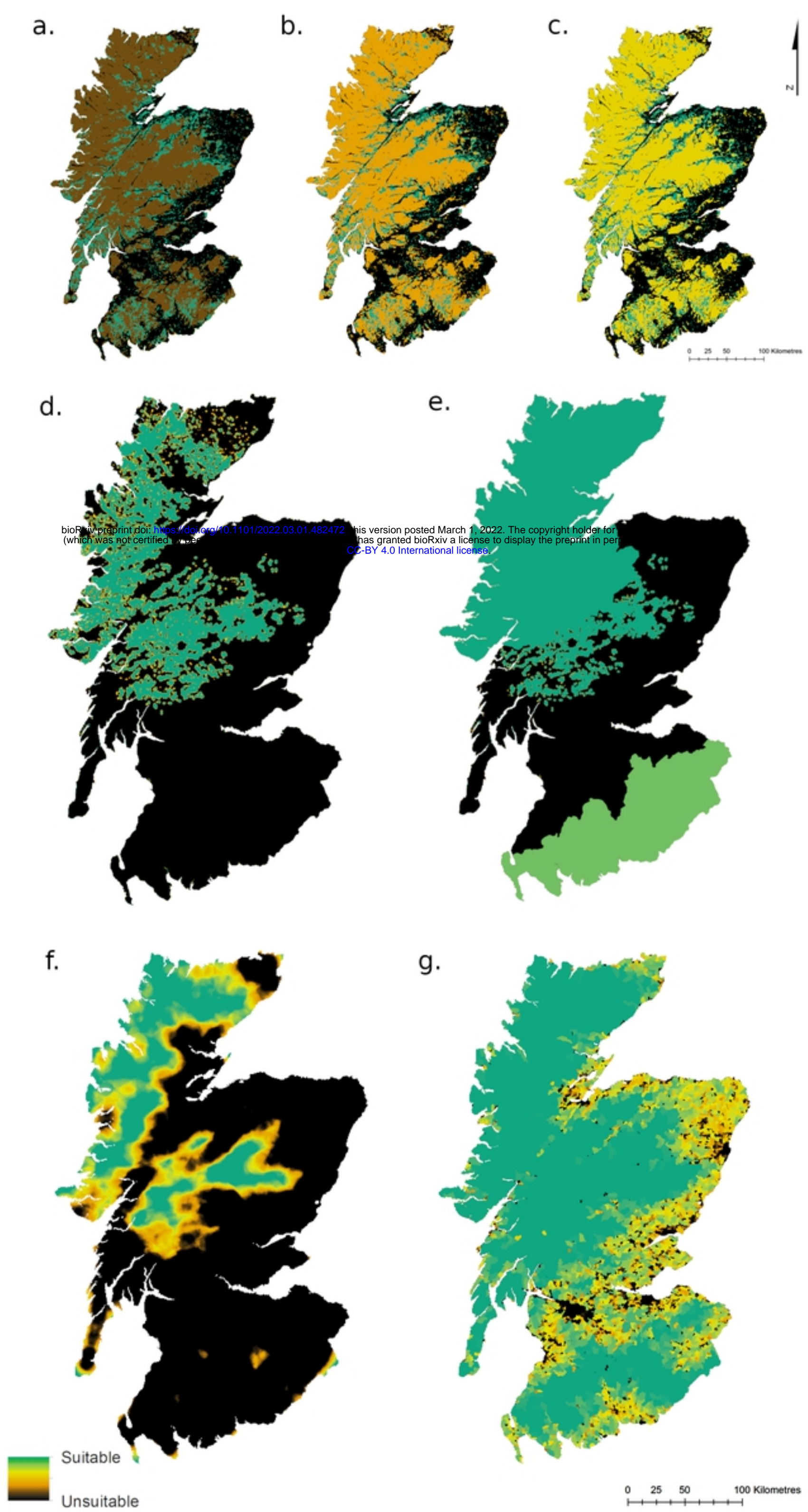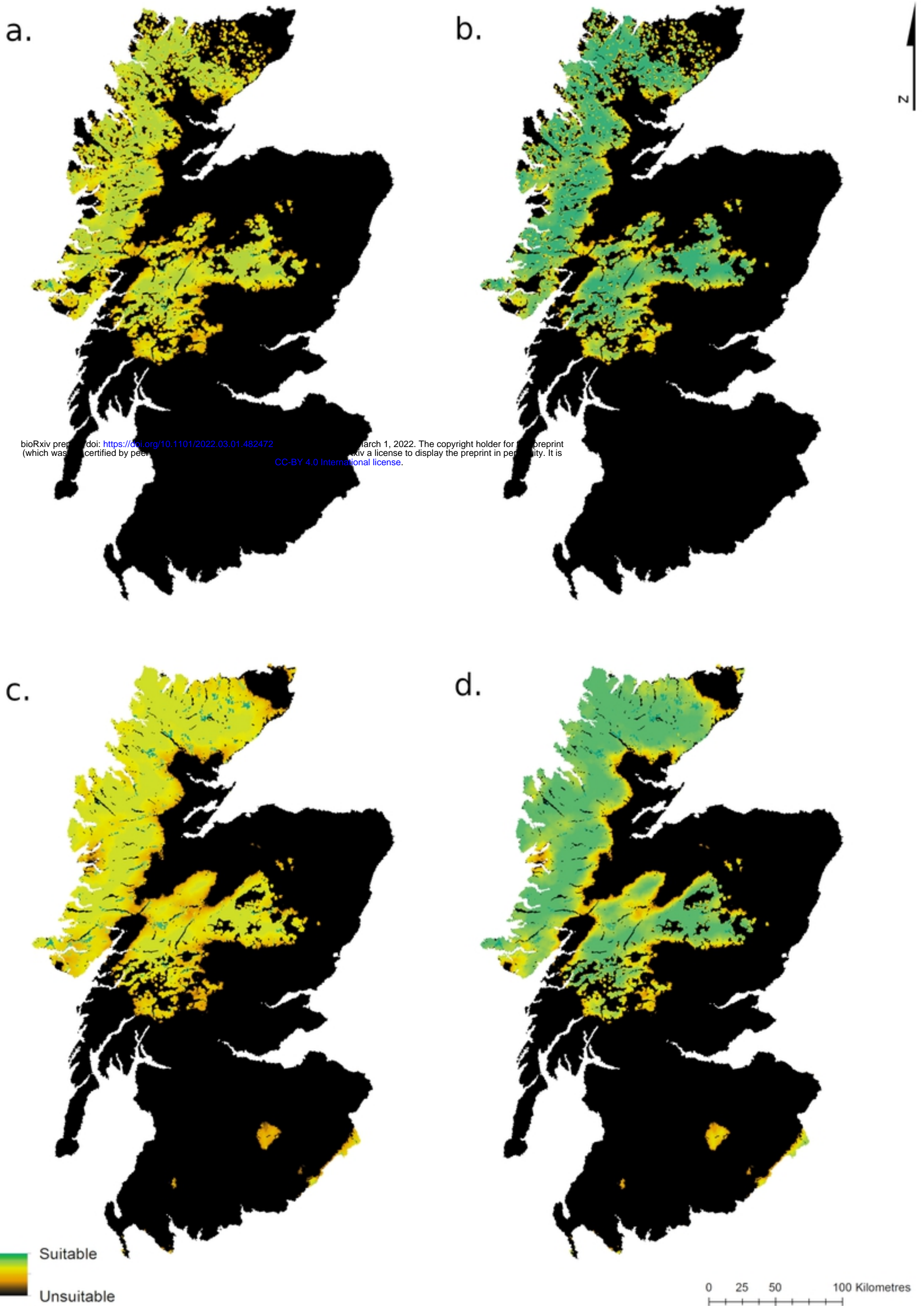
29

Figure 1

Figure 2

Suitable

Unsuitable

Figure 3

Figure 4

Area in Each Percentile of Suitability

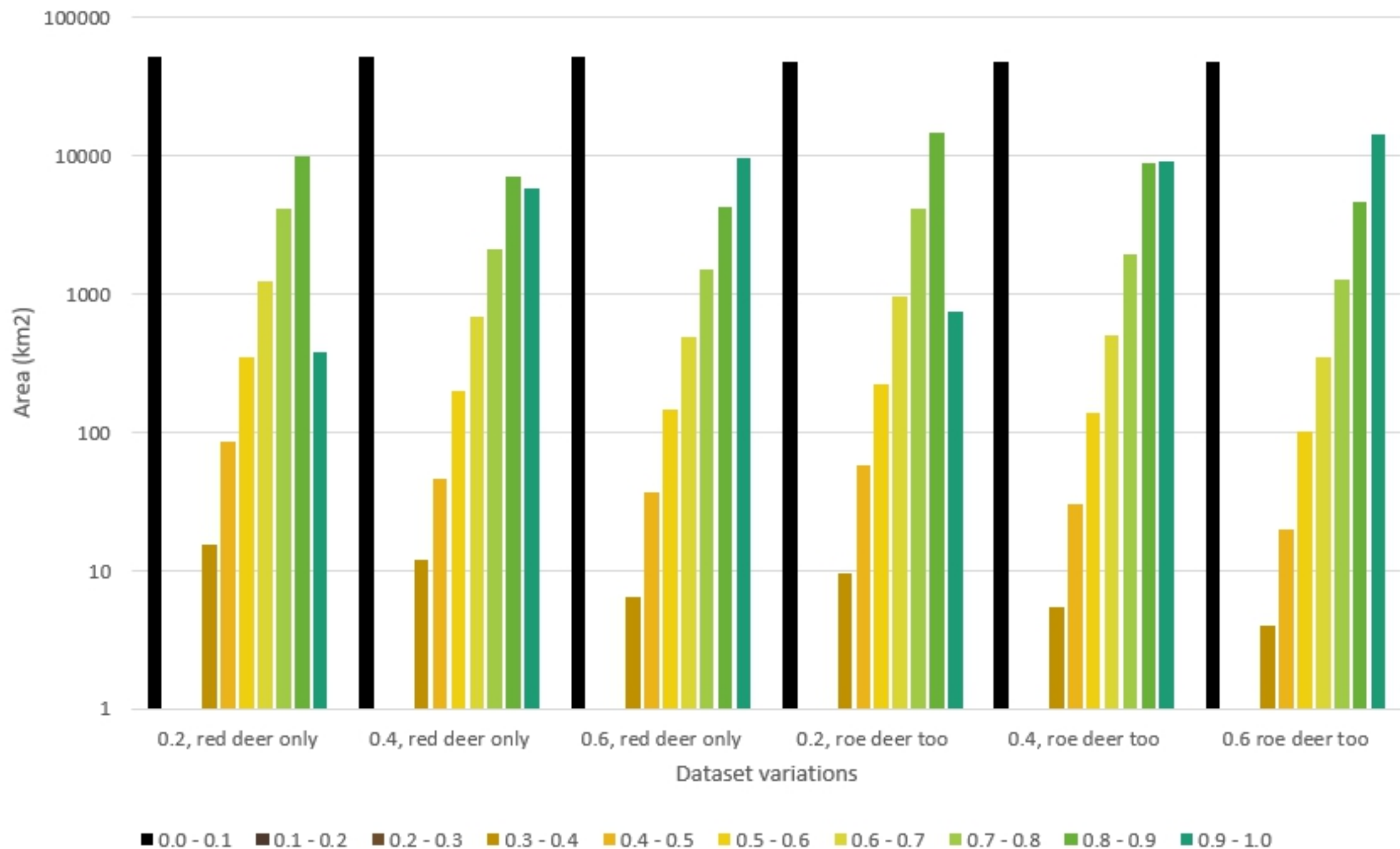Figure 5