

# Landscape effects on wild boar home range size under contrasting harvest regimes in a human-dominated agro-ecosystem

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**Abstract** Agro-ecosystems can experience elevated human-wildlife conflicts, especially crop damage. While game management often aims at reducing number to mitigate conflicts, there is on-going debate about the role of hunting disturbance in promoting game to range over wider areas, thereby potentially exacerbating conflicts. Herein, we hypothesised that landscape configuration and non-lethal disturbance modulate the response to harvest disturbance. We used an information theoretic approach to test the effects of landscape and anthropogenic variables on wild boar ranging patterns across contrasting harvest regimes. We used 164 seasonal home ranges from 95 wild boar (*Sus scrofa*) radio-tracked over 6 years in the Geneva Basin where two main harvest regimes coexist (day hunt and night cull). Mean seasonal 95% kernel home range size was  $4.01 \pm 0.20 \text{ km}^2$  (SE) and 50% core range size  $0.79 \pm 0.04 \text{ km}^2$ , among the smallest recorded in Europe. Range sizes were larger in the day hunt area than in the night cull area, with no seasonal effect. However, when accounting

for landscape variables, we demonstrate that these patterns were likely confounded by the underlying landscape configuration, and that landscape variables remain the primary drivers of wild boar ranging patterns in this human-dominated agro-ecosystem with range size best explained by a model including landscape variables only. Therefore, we recommend accounting for landscape configuration and sources of non-lethal disturbance in the design of harvest strategies when the aim is to limit wide-ranging behaviour of wild boar in order to mitigate conflicts.

**Keywords** Culling · Disturbance · Fragmentation · Home range · Hunting · *Sus scrofa*

## Introduction

Agro-ecosystems can experience high abundance of wild game species (Hebeisen et al. 2008), especially if food is abundant year-round (Schley and Roper 2003), natural predators have been extirpated (Ripple and Beschta 2012), or milder winters increase game survival (Vetter et al. 2015). High abundance can intensify human-wildlife conflicts, such as disease spill-over to domestic stock (Wu et al. 2011), zoonosis (Meng et al. 2009), road casualties (Morelle et al. 2013), or crop damage (Amici et al. 2011; Schley et al. 2008). While management usually aims at reducing population size through harvest, it often ignores landscape structure and fragmentation that affect home range size (Bevanda et al. 2015), or behavioural responses to mortality risk and non-lethal disturbance that could either exacerbate or help mitigate conflicts (Cromsigt et al. 2013).

Ranging patterns reflect the distribution of resources, and the trade-off animals make between the benefits of exploiting them and the risks associated with accessing them. Home range

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placement and habitat use are therefore driven by the need to balance access to limiting resources (Mysterud and Ims 1998), and avoidance of predation risk (Fortin et al. 2005) or human disturbance (Selier et al. 2015). Therefore, temporal and spatial variation in resource availability, such as altitudinal gradients or habitat configuration (landscape hypothesis; Bevanda et al. 2015), and in mortality risk (behavioural response to risk hypothesis; Tolon et al. 2012), or non-lethal disturbance (behavioural response to disturbance hypothesis; Muhly et al. 2011) should lead to changes in home range size.

Area minimisation through foraging optimality should lead animals to adjust their range size to landscape configuration in order to include limiting resources (Mysterud and Ims 1998). However, animal may range more widely to avoid disturbance. While some human recreational activities can create spatial refuges that favour prey species over their predators (Muhly et al. 2011), harvest likely creates risk and disturbance that affect animals' space use in a fashion analogous to the fear of predation (Lone et al. 2014; Tolon et al. 2009). Heterogeneous landscapes provide solutions to the risk-forage trade-off, such as the use of refuges (Jachowski et al. 2012; Tolon et al. 2012). In a given fragmented landscape, larger home ranges are likely more heterogeneous than smaller home ranges (Beyer et al. 2010), and likely offer more spatial solutions to the risk-forage trade-off at a given time than more homogeneous, smaller home ranges (Forman 1995).

Wild boar (*Sus scrofa*) behavioural plasticity enables them to thrive in human-dominated landscapes (Cahill et al. 2012), and they are now considered as a pest throughout most European agro-ecosystems (Massei et al. 2015). Wild boar ranging patterns can be affected by seasonal availability of food or cover, or level of anthropogenic disturbance (Keuling et al. 2008a; Podgórski et al. 2013; Saïd et al. 2012; Scillitani et al. 2010; Thurfjell et al. 2013). In particular, there is on-going debate about the role of disturbance during traditional drive hunts in promoting wild boar to range over a wider area, thereby exacerbating conflicts, compared to other methods. However, previous studies of the effect of hunting methods on wild boar space use often ignored the possible influence of other source of human disturbance, such as recreational activities, or landscape configuration on wild boar spatial behaviour, drawing conflicting conclusions (Keuling et al. 2008b; Scillitani et al. 2010).

To address this research gap, we used 6 years of wild boar telemetry data from the Geneva Basin to measure wild boar home range and core area size under two contrasting harvest regimes, while accounting for landscape variables. We predicted that range size would increase with level of harvest disturbance, but that this effect would be modulated by landscape configuration and non-lethal disturbance. We developed a set of alternative *a priori* hypotheses to test for different combinations of the variables associated with harvest disturbance, non-lethal disturbance and landscape configuration (Table 1).

**Table 1** *A priori* hypotheses and corresponding candidate models exploring the effect of harvest regimes, season, human disturbance and landscape characteristics on home range and core range size of wild boar in the Geneva Basin, 2002–2007

Hypothesis	Model structure <sup>a</sup>
Null model	Area ~ 1
Harvest regime	Area ~ season × regime
Forest configuration	Area ~ npFOR + adjFOR
Cropland configuration	Area ~ npAGR + adjAGR
Topography	Area ~ mELE
Human access	Area ~ dHum
Refuge	Area ~ pPro
Landscape	Area ~ npFOR + adjFOR + npAGR + adjAGR + mELE
Landscape and harvest regime	Area ~ season × regime + npFOR + adjFOR + npAGR + adjAGR + mELE
Human disturbance	Area ~ pPro + dHum
Human disturbance and harvest regime	Area ~ season × regime + pPro + dHum
Landscape and human disturbance	Area ~ npFOR + adjFOR + npAGR + adjAGR + mELE + pPro + dHum
Full model	Area ~ season × Reg + npFOR + adjFOR + npAGR + adjAGR + mELE + pPro + dHum

<sup>a</sup> Structure of the fixed effects. All models were fitted with random intercepts for individuals nested within groups and a random intercept for the year of sampling. *Reg* harvest regime (categorical), *pPro* proportion of protected land, *dHum* average distance to human settlements, *npFOR* number of forest patches, *adjFOR* percent-like-adjacency of forest patches, *npAGR* number of crop patches, *adjAGR* percent-like-adjacency of crop patches, *mELE* mean elevation

## Material and methods

### Study area

We studied wild boar space use at three study sites in the Geneva Basin (680 km<sup>2</sup>), centred on the France-Switzerland border (N 46° 30', E 6° 30') between 2002 and 2007. The Basin is delimited by wooded mountain ridges, and the western tip of Lake Geneva (Fig. 1). About 700,000 people inhabit the Basin, with ca. 500,000 inhabitants in Geneva agglomeration at its core. Lowlands (350–600 m asl) are a mosaic of built-up areas, cropland (mostly vineyards, wheat and maize) and fragmented forests. Large carnivores are absent from the Basin, and the study area harbours one of the highest wild boar density in Europe (>10 ind./km<sup>2</sup>; Hebeisen et al. 2008). Boar harvest occurs in autumn and winter (September–February), and two main wildlife management and harvest regimes co-exist in the Basin (see *Harvest regimes* below).

### Capture and tracking

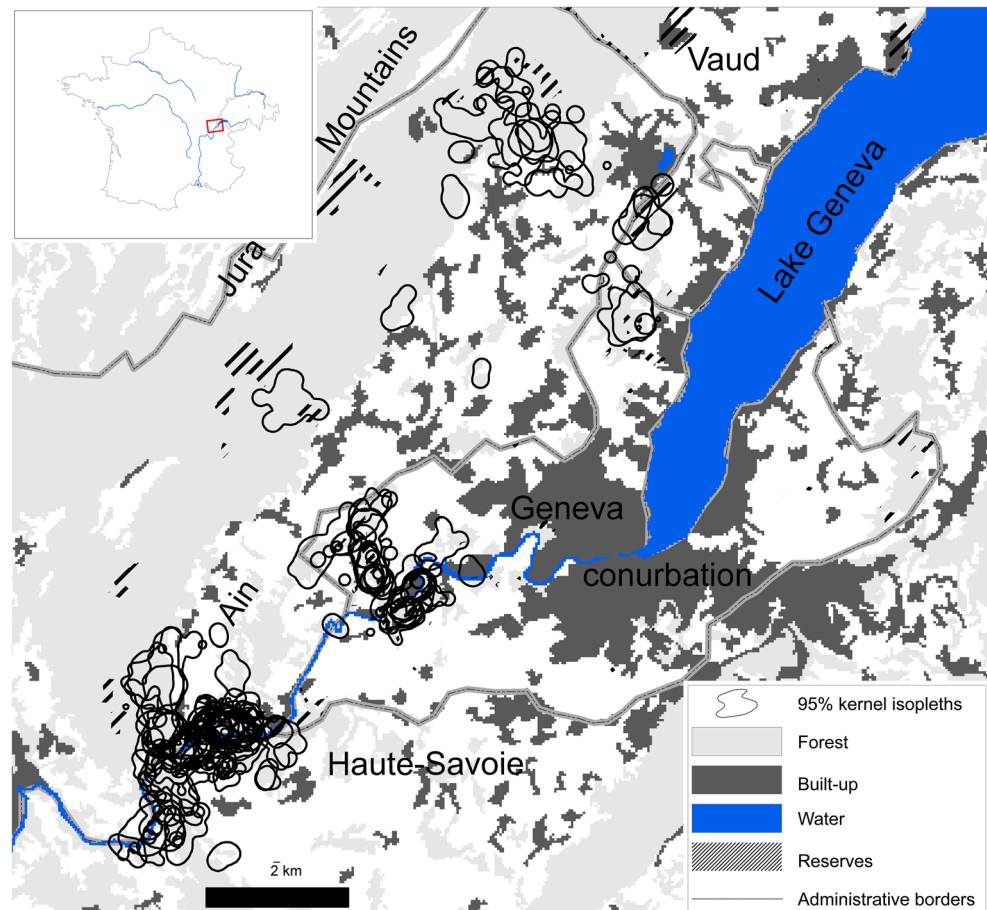
We captured wild boar using maize-baited live-traps (Fischer et al. 2004). We only anaesthetised individuals >80 kg using Zoletil prior to handling (Fournier et al. 1995). We outfitted

females <60 kg and males <100 kg either with VHF collars (ATS, USA, 200 g) using extensible belting (Brandt et al. 2004), or with VHF transmitters (Biotrack, UK, 40 g) glued on cattle ear tags. We outfitted females >60 kg and males >100 kg with VHF radio-collars (ATS, USA, 200 g). All individuals were released at the capture site. We radio-tracked wild boar on the ground and estimated their position using triangulation. Twice weekly, on average, we located every radio-tagged individual at 3-h intervals five times during their active foraging period between 18:00 h and 06:00 h. At various time intervals, we recorded diurnal resting location, mainly between 09:00 h and 15:00 h.

### Home range analysis

Based on harvest, we defined two 6-month seasons: non-harvest season (March–August) and harvest season (September–February). Because adult males were too few ( $n = 9$ ) to test for a difference in ranging patterns between solitary adult males and group living individuals, we restricted our analysis to group-living individuals with  $\geq 30$  relocations in a given season. We computed fixed kernel utilisation distribution (UD; Worton 1989) using the package *adehabitatHR* (Calenge 2006) in the R environment (R Core Team 2016).

**Fig. 1** Seasonal 95% kernel wild boar home ranges during the harvest season in the Geneva Basin, 2002–2006. *Inset* shows the location of the study area on the France-Switzerland border. Landuse background is based on Corine land cover label 1 level



This estimator is suitable for relatively scarce, temporarily independent data (Kernohan et al. 2001), and is suitable for comparing relative range sizes across individuals and time (Signer et al. 2015). We used a smoothing factor bandwidth  $h$  of 200 m, consistent with our relocation error. We defined home ranges and core ranges as the 95 and 50% kernel UD isopleths, respectively. We also report 95 and 50% minimum convex polygon (MCP; Hayne 1949) seasonal range size for comparison with the literature (Appendix S1).

### Landscape configuration and fragmentation variables

We used CORINE landcover data (100-m resolution; European Environment Agency 2006) to characterise the landscape. We reclassified land cover categories based on label 1 level into 5 categories: (i) artificial surfaces, (ii) agricultural areas, (iii) forest and semi natural areas, (iv) wetlands and (v) water bodies. All other environmental variables were resampled at the resolution of the CORINE landcover.

Based on previous studies on the effect of landscape configuration on ungulate home range size (Bevanda et al. 2015; Dechen Quinn et al. 2013; Saïd and Servanty 2005), we used FRAGSTATS (McGarigal et al. 2002) to extract metrics of forest and cropland configuration within ranges. Within each individual seasonal home range and core range, we computed the proportion of forest, and of crop, the number of patches of forest, and of crop, and the mean patch size of forest, and of crop. As an index of fragmentation, we extracted the percent-like-adjacency of forest, and of crop patches. Percent-like-adjacency is the proportion of patches adjacent to another patch of the same landcover class (aggregation) and ranges between zero (every cell of a given landcover is a different, discrete patch) and 1 (all cells of the same landcover consist of a single patch; McGarigal et al. 2002).

To account for topography, we computed elevation and terrain ruggedness (difference between elevation of a cell and the mean elevation of the neighbouring 8 cells) based on a digital elevation model (EU-DEM Copernicus 2013) using the R package *raster* (Hijmans and Eten 2012). We then averaged all elevation or ruggedness values within an individual's home range and core range.

### Disturbance variables

To account for anthropogenic disturbance, we assessed home range proximity to anthropogenic infrastructures: we extracted the distance of each  $100 \times 100$  m cell to the closest artificial surfaces and the distance to each of the following linear features: distance to railways, freeways, primary roads, minor roads, and hiking trails and paths (source: [www.openstreetmap.org](http://www.openstreetmap.org)). For data analysis, we calculated the mean value of these variables within each individual range.

### Harvest regimes

Based on the location of their core range relative to administrative limits, we identified which harvest regime wild boar were exposed to (Fig. 1). We defined two levels to the variable *regime*: *night cull* (in Geneva) and *day hunt* (in France and Vaud). In canton Geneva, Switzerland, hunting was abolished in 1974. In autumn and winter (September–February), wild boar culls are carried out solely by game warden outside forested areas, with the aim of controlling population size and limit crop damage. Wardens exclusively shoot wild boar at night, using a night vision scope from a vehicle. In the surrounding French departments Ain and Haute-Savoie, and Swiss canton Vaud, traditional diurnal hunts occur between September and February. In the two French departments, dogs and beaters are used to drive wild boar towards shooting lines (Tolon et al. 2012), and in Vaud tracking is carried out by smaller groups of hunters, with dogs. In this study, we qualitatively defined disturbance by daytime drive hunts to be higher than night-time culls. To account for possible refuge effect of protected areas with no harvest under either regime, we calculated the proportion of home range overlap with protected areas (*pPro*).

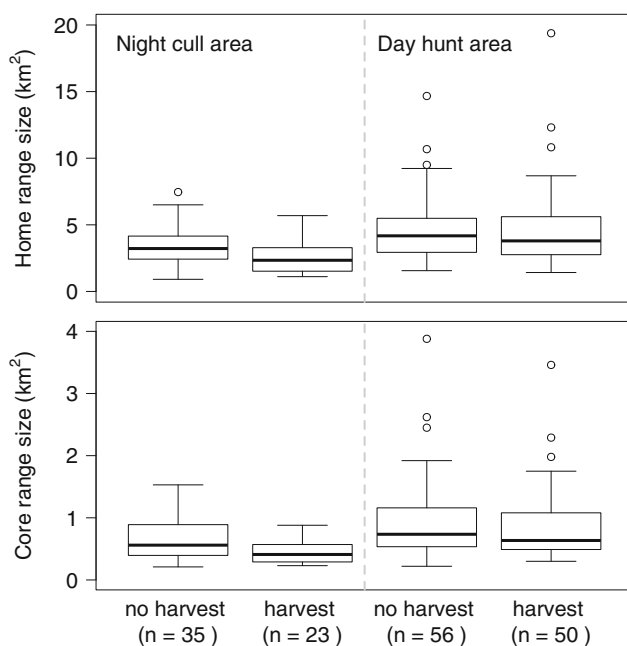
### Statistical analysis

We screened the exploratory variables for collinearity using a cut-off Spearman's  $|r| = 0.6$ . Among collinear variables, we retained the one with the greatest  $R^2$  in a univariate linear regression of range size. We retained number of patches of forest (*npFOR*) and crop (*npCROP*), percent-like-adjacency of forest (*adjFOR*) and crop (*adjCROP*), mean elevation (*mELE*), mean distance to artificial surfaces (*dHUM*), proportion of range area protected (*pPro*) and harvest *regime* in interaction with *season* to build a set of generalised linear mixed-effect models (GLMMs; Bolker et al. 2009) with a Gaussian link for testing *a priori* hypotheses of the effects of harvest regimes, harvest season, human disturbance and landscape features on wild boar ranging patterns (Table 1). To account for pseudoreplication of individuals and groups sampled repeatedly, we fitted each model of home range or core range size with random intercepts for individuals nested within groups. We also fitted random intercepts for the years of sampling to account for annual environmental variations (e.g. climatic), which we did not explicitly measure. We used the Akaike's information criterion corrected for small sample size (AICc) in an information theoretic framework to select for the most parsimonious candidate models within  $<2$  AICc (Burnham and Anderson 2002). Fixed effect coefficients in the final model were deemed significant when the corresponding 95% confidence interval (95% CI) did not overlap zero. We fitted GLMMs using the *lme4* package (Bates et al. 2013) in R version 3.3.2 (R Core Team 2016).

## Results

We obtained 164 seasonal ranges from 95 wild boar (20 sub-adult males, 75 subadult and adult females) in 68 sounders. We tracked wild boar on average during  $126.4 \pm 3.4$  days per season, over 1–10 seasons. Overall, mean seasonal home range size was  $4.01 \pm 0.20$  km<sup>2</sup> (SE) (range: 1.11–7.46 km<sup>2</sup>). Mean home range size in the night cull area was  $2.54 \pm 0.24$  km<sup>2</sup> (1.11, 5.69) during the harvest season and  $3.40 \pm 0.25$  km<sup>2</sup> (0.91, 7.46) during the non-harvest season. In the day hunt area, mean home range size was  $4.66 \pm 0.44$  km<sup>2</sup> (1.42, 19.38) during the harvest season and  $4.56 \pm 0.33$  km<sup>2</sup> (1.56, 14.67) during the non-harvest season (Fig. 2). Home ranges in the day hunt area were larger than in the night cull area ( $\beta = 1.35$ ; CI 0.46, 2.23), with no significant effect of *season*, either univariately ( $\beta = -0.03$ ; CI -0.69, 0.62) or in interaction with harvest *regime* ( $\beta = 0.92$ ; CI -0.46, 2.30).

When accounting for other sources of anthropogenic disturbance and landscape variables, home range size was best explained by a model including landscape variables only (Table 2), with significant effects of *npFOR* ( $\beta = 0.45$ ; CI 0.34, 0.55), *adjFOR* ( $\beta = 5.46$ ; CI 2.76, 8.12), *npCROP* ( $\beta = 0.41$ ; CI 0.31, 0.50), *adjCROP* ( $\beta = 4.66$ ; CI 2.70, 6.60) and *mELE* ( $\beta = 0.006$ ; 0.004, 0.008; Fig. 3a). Standardised fixed effect coefficient showed stronger effects of *npFOR*, *npCROP* and *mELE* relative to *adjFOR* and *adjCROP* (Fig. 4a).



**Fig. 2** Wild boar 95% kernel home range and 50% kernel core range size under two harvest regimes during the no harvest and the harvest seasons<sup>a</sup> in Geneva Basin, 2002–2007. <sup>a</sup>Harvest season: September 1st to February 28/29 (autumn and winter); non-harvest season: March 1st to August 31 (spring and summer)

Overall, mean seasonal core range was  $0.79 \pm 0.04$  km<sup>2</sup> (0.21, 1.53). Results of the core range analyses showed similar results to the home range analyses, and details are reported in Table S2 and Appendix 3. A landscape-only model ranked first (Table S2), with the effects of *npCROP* ( $\beta = 0.02$ ; CI -0.02, 0.06), and *adjCROP* ( $\beta = 0.08$ ; CI -0.17, 0.33) being non-informative in the final model (Fig. 3a). Standardised fixed effect coefficient showed a stronger effect of *mELE*, and *npFOR* relative to *adjFOR*, with *npCROP* and *adjCROP* being non-informative (Fig. 4b).

## Discussion

We demonstrate that the landscape configuration is primarily driving the patterns of wild boar range size we observed, in support to our landscape hypothesis, and that the apparent effect of different harvest regimes was likely confounded by landscape variables, and the mortality risk and disturbance hypotheses were not supported. Wild boar home ranges in the Geneva Basin were among the smallest recorded in Europe (see Keuling et al. 2007 for a review). Small home range size was congruent with the wild boar population density in the Geneva Basin being among the highest in Europe at the time of the study (Hebeisen et al. 2008). We studied wild boar in a human-dominated agro-ecosystem and expected range size to be small because of abundant food resources provided by crops year-round (Keuling et al. 2008a). The largest home ranges were located at higher elevation, consistent with resource dispersion with altitude (Burt 1943).

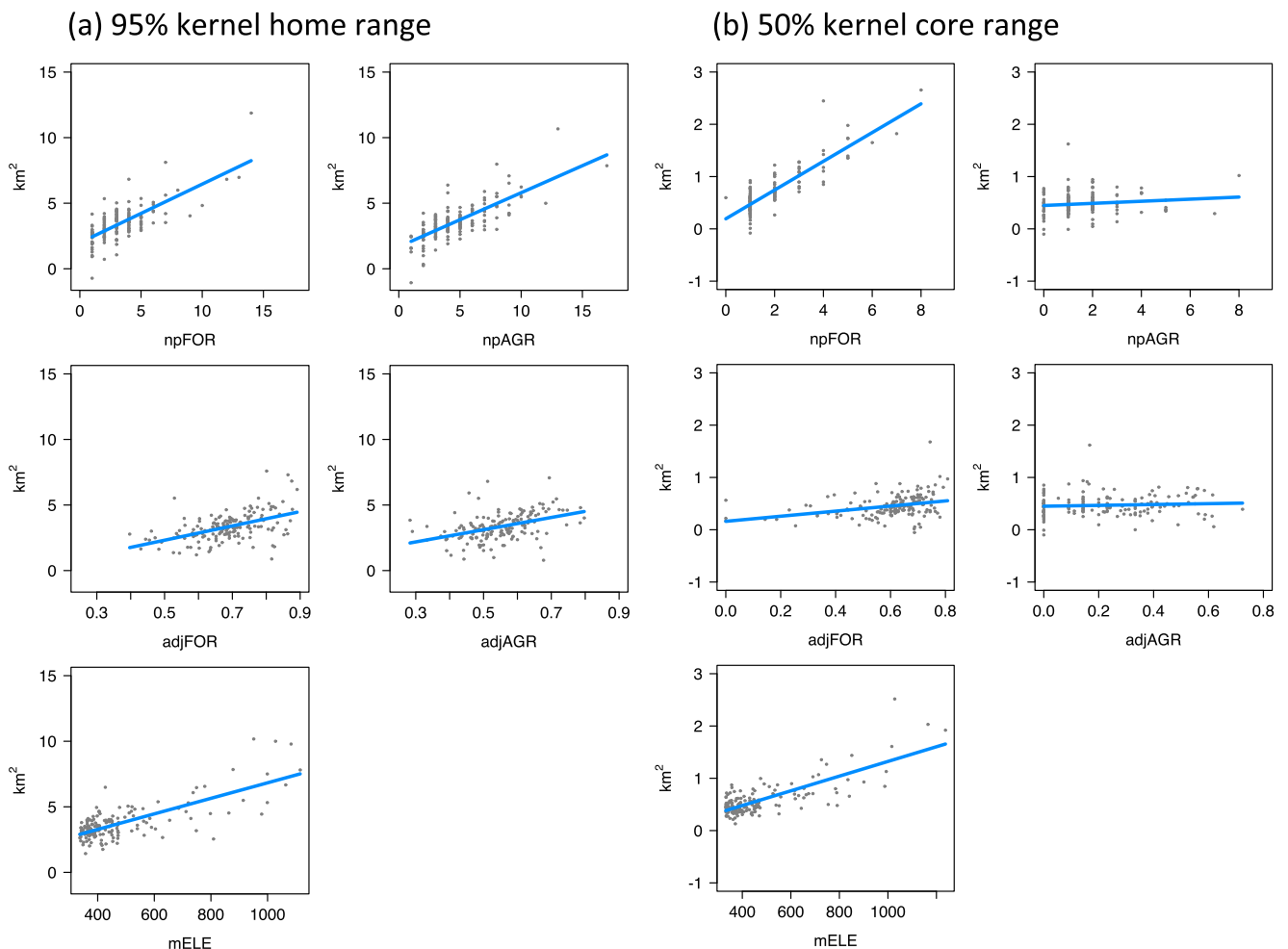
At first, harvest regime appeared to affect home range and core range size, with ranges being larger in the day hunt area than in the night cull area (Fig. 2). Such patterns of wider ranging in response to disturbance of drive hunts have often been documented in wild boar (Keuling et al. 2008b; Scillitani et al. 2010; Thurfjell et al. 2013). However, the lack of seasonal effect indicated on the contrary no influence of harvest season on the ranging behaviour of wild boar, with range size being stable throughout the year. However, we acknowledge that effects of harvest season could be confounded with phenology of habitats (Keuling et al. 2008a). Wild boar culling and hunting occurred in autumn and winter, during and after crop harvest, when mast became available. Although irregular in intensity, mast availability in forests could favour ranging behaviour constrained to this type of habitat, which also offers suitable cover for resting (area minimisation around limiting resources; Mysterud and Ims 1998). Alternatively, effects of harvest disturbance on ranging patterns may persist over time (Fattebert et al. 2016), masking putative differences driven by habitat phenology.

When accounting for landscape variables, however, landscape effects overrode these apparent effects of harvest regimes on wild boar range size. Forest and cropland

**Table 2** Results of the selection of *a priori* models of wild boar 95% kernel home range size wild boar in Geneva Basin, 2002–2007

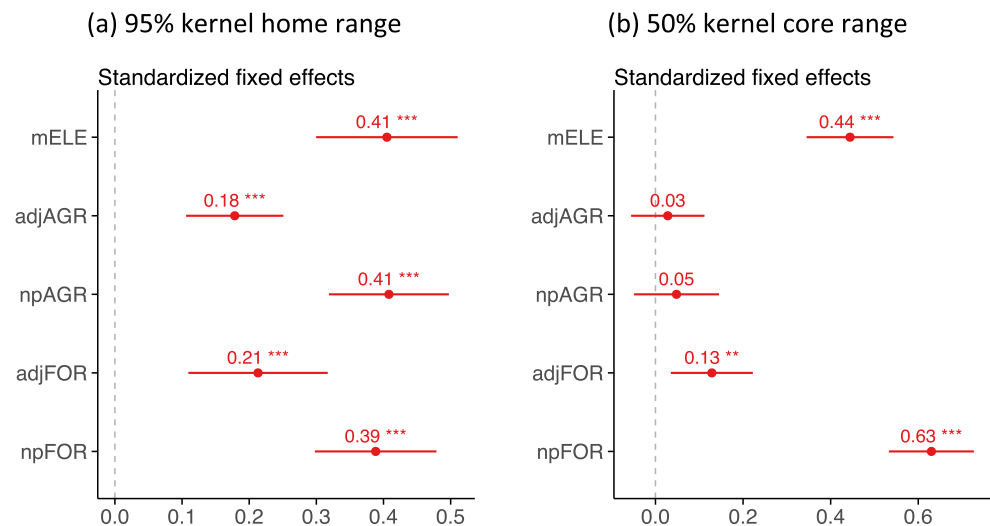
Model	K	LL	AICc	$\Delta AICc$	AICcWi
Landscape	10	-246.74	514.92	0	0.84
Landscape and human disturbance	12	-246.27	518.61	3.68	0.13
Landscape and harvest regime	13	-246.65	521.73	6.8	0.03
Full model	15	-246.17	525.59	10.66	0
Forest configuration	7	-296.41	607.54	92.62	0
Cropland configuration	7	-323.21	661.15	146.22	0
Human disturbance	7	-348.15	711.01	196.09	0
Human disturbance and harvest regime	10	-345.7	712.83	197.91	0
Topography	6	-350.94	714.42	199.5	0
Human access	6	-355.11	722.76	207.84	0
Refuge	6	-362.29	737.11	222.18	0
Harvest regime	8	-368.75	754.43	239.5	0
Null model	5	-373.93	758.24	243.31	0

*K* number of parameters, *AICc* Akaike information criteria adjusted for small sample sizes,  $\Delta AICc$  (*AICc*–(*AICc*)<sub>min</sub>), *w<sub>i</sub>* Akaike weight



**Fig. 3** Effect of number of forest patches (*npFOR*), number of crop patches (*npAGR*), percent-like-adjacency of forest patches (*adjFOR*), percent-like-adjacency of crop patches (*adjAGR*) and mean elevation (*mELE*) on wild boar home range (a) and core range (b) size in Geneva Basin, 2002–2007. Grey dots depict partial residuals of the multiple regression for each variable

**Fig. 4** Standardised coefficients of the effect of forest patches (*npFOR*), number of crop patches (*npAGR*), percent-like-adjacency of forest patches (*adjFOR*), percent-like-adjacency of crop patches (*adjAGR*) and mean elevation (*mELE*) on wild boar home range (a) and core range (b) size in Geneva Basin, 2002–2007. Error bars depict standard error of the standardised coefficients



configuration played the most important role in driving wild boar ranging patterns in this fragmented landscape, in conjunction with topography. Wild boar use crops seasonally (Keuling et al. 2008a), and it is often argued that wild boar range spread and population increase in Europe over the last four decades have been favoured by the availability of abundant food resources in croplands (Geisser and Reyer 2005; Rosell et al. 2012), coupled with hunting inefficiency (Keuling et al. 2013; Massei et al. 2015). However, forest configuration and elevation appeared to be stronger drivers of wild boar ranging patterns than cropland configuration (Fig. 4a), stressing the importance of forest habitat in agroecosystems for this species. A recent study of the recolonisation of its former range by wild boar over a 30-year period in southern Belgium, albeit at a coarser landscape scale, showed that wild boar are more likely to colonise areas where forest dominates (Morelle et al. 2016). Also at the core range level, forest configuration and elevation drove wild boar ranging patterns, with no significant effect of crop configuration (Fig. 4b). This possibly indicates less plasticity at the core range level, the part of a home range most important for the acquisition of limiting resources, e.g., resting sites, essential for survival, and reproduction (Kernohan et al. 2001).

We found no effect of non-lethal human disturbance such as measured by proximity to infrastructures, or a refuge effect of protected area on range sizes. A previous study at finer scale around a nature reserve in the French Department Ain showed that wild boar were using the reserve as a refuge when hunting occurred up to 2 km from the edge of the protected area (Tolon et al. 2009; Tolon et al. 2012). Finer scale movements are also likely more affected by crop availability, both in time and space (Keuling et al. 2008a).

Here, we focused on the factors driving ranging patterns, i.e., home range and core range size over a coarse spatial-temporal scale, and not habitat selection *per se*. In particular,

we did not analyse within-home range habitat selection. Resource availability is scale-dependent (Beyer et al. 2010), and selection patterns vary across spatial or temporal scales (Meyer and Thuiller 2006). Also, distinction between different behaviours or movement patterns is becoming central in resource selection studies (Fattebert et al. 2015; Morelle et al. 2015). Thus, conducting resource selection analyses distinguishing between nocturnal (active foraging period) and diurnal (resting) selection patterns would likely further improve our understanding of space use strategies of wild boar under contrasting management regimes to better inform management protocols in accounting for habitat heterogeneity across a gradient of harvest regimes (Cromsigt et al. 2013; Keuling et al. 2008b). Also, more data on adult solitary males would be needed to allow for explicit testing of putative effects of harvest regimes and landscape on ranging patterns in this age-sex class.

## Conclusion

While wild boar range size appeared to be driven by harvest regimes (Fig. 2), we demonstrated that these patterns were likely confounded by the underlying landscape configuration, and that landscape variables remain the primary drivers of wild boar ranging patterns in this human-dominated agro-ecosystem. In particular, forest configuration appeared to be an essential driver of both home range and core range size. Topographic variables, likely correlated with resource availability, are also good predictors of home range and core range size in this landscape. Our study therefore highlights the need to take landscape variables into account when assessing the effect of management regimes on animal space use as the former might prevail over the latter.

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