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Invading or recolonizing? Patterns and drivers of wild boar population expansion into Belgian agroecosystems



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ABSTRACT

Native species can also exhibit invasive-like spreading patterns, and identifying mechanisms driving spread of native species is a recent but essential challenge in ecology. In Europe, wild boar *Sus scrofa* populations and range increased for decades. While patterns of population growth are well studied, those related to range expansion are still poorly understood. In this study, we aimed to understand patterns and mechanisms that promoted wild boar population expansion in agricultural landscapes of Southern Belgium between 1981 and 2010. Using hunting-based knowledge on colonization history and an information-theoretic approach, we evaluated support to four *a priori* hypotheses explaining mechanisms of wild boar colonisation in an agro-ecosystem: natural forested landscape as recolonization mechanism, and cultivated landscape, propagule pressure and climate change as invasion mechanisms. We found that wild boar population expansion in Belgian agroecosystems was a relatively slow process driven by the natural landscape, propagule pressure, and climatic changes. This suggests a combination of invasive and recolonization mechanisms was in play in the expansion of wild boar over the last three decades. Our study provides insights in the mechanisms that enable the species' recovery in Europe since the mid-20th century, and underline the need for adapted management strategies taking into account the invasive components of wild boar population expansion.

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1. Introduction

Species distribution is driven by the risk-forage trade-off, dispersal abilities and climatic factors (Franklin and Miller, 2009; Guisan and Thuiller, 2005). Since ecosystems are continuously under natural and human influences, e.g. climatic conditions or land use practices, species' niche must be considered as a dynamic trait of a species (Pearman et al., 2008). Range occupancy can either increase or decrease, depending on the species' requirements and ability to respond to changing conditions. Modification to landscape structure and composition, propagule pressure, climate change, and habitat suitability are important drivers of the successful establishment and expansion of invasive species (Lockwood et al., 2005).

Most studies of spread of organisms are traditionally devoted to exotic species becoming invasive. However, changes in environmental conditions can also lead native species to increase their

occupied range and demonstrate an invasive-like behavior (Buczkowski, 2010). After obstacles to its proliferation disappeared, a native species can display invasive-like traits such as rapid spread, occupancy of novel areas, dominance in the ecosystem, and can be defined as a 'native invasive species' (Valéry et al., 2009a), or 'native invaders' (Simberloff and Rejmanek, 2010). Despite increased interest (Carey et al., 2012; Valéry et al., 2009b), studies of native population spread yet remain largely undocumented and consequently poorly understood. In order to prevent negative impacts caused by some native species and implement effective management strategies, it is also crucial to disentangle the mechanisms influencing the spread of native animal populations. Identification of factors favoring spread of native species is indeed central to the design of human-wildlife conflict mitigation strategies, including dealing with over-abundance (Cromsigt et al., 2013; Gortázar et al., 2006).

We used wild boar *Sus scrofa* population expansion in Belgian agroecosystems observed over the last 30 years as a model for investigating spreading mechanisms. Wild boar are raising numerous ecological and socio-economical concerns in its Eurasian native range (Massei and Genov, 2004; Putman et al., 2011). With highly adaptive life-history traits (Gamelon et al., 2013,

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2011) and a generalist diet (Herrero et al., 2006; Schley and Roper, 2003), wild boar exploit a large range of food sources, and occur under various environmental conditions. While demographic recovery of wild boar in its native Eurasian range has been acknowledged for decades (Saez-Royuela and Telleria, 1986), mechanisms of range expansion, and the suite of factors favoring the species spread remains poorly understood. Specifically, we modeled the probability of an unoccupied 10×10 km grid cell to be colonized by wild boar at 5-year time intervals. We documented wild boar range expansion, and we used an information-theoretic approach to assess support for four *a priori* hypotheses (H) and corresponding predictions (P) of putative drivers (Table 1). As wild boar is predominantly a forest-dwelling species (Briedermann, 1990), we tested a 'natural landscape' hypothesis (H1), predicting that forest habitat favors population spread (P1). Borrowing the concept from invasion ecology that the number of individuals involved in the invasion is a pivotal predictor of invasion success (Lockwood et al., 2005), we tested a 'propagule pressure' hypothesis (H2), and predicted that neighbouring presence favors spread into unoccupied areas through density-dependent dispersal (P2) (Gaston et al., 2000). Following changes in European agriculture practices since the 1980s, i.e. increase in maize and rapeseed cultivations (Anonymous, 2012), we tested a 'cultivated landscape' hypothesis (H3), predicting that increased crop cover favored wild boar spread and occupancy of agroecosystems (P3). Finally, we developed a 'climate change' hypothesis (H4) to test for putative effects of increased temperature favoring northwards range shifts over the last decades (Thomas et al., 2001). Considering the relatively small spatial and short time scales of our study, we predicted that climate did not play a role in the spread of wild boar population (P4).

2. Material and methods

2.1. Study area

Discovery of wild boar remains up to the North sea attest to the historical presence of the species over the entire territory of modern Belgium until the Middle age (ca. AD 1500) (Toussaint, 2011). Between AD 1500 and AD 1850, forest clearance for the development of agriculture, together with human population increase and the concomitant rise in hunting pressure restricted the range of many forest-dwelling species in Europe (Kaplan et al., 2009). Wild boar consequently disappeared from many parts of its native range (Danilov and Panchenko, 2012). In Belgium, wild boar distribution became restricted to the forested areas of the Ardenne region in the south until the mid-20th century. Since the 1980s, wild boar population has progressively started to expand northwards and to colonize agroecosystems of Southern Belgium (Morelle and Lejeune, 2014). In these agroecosystems, hunting traditionally targets small game species (i.e. rabbits, hares, pheasant). Consequently, wild boar return is not considered positively by most hunters and farmers in these areas, and wild boar are mostly hunted with the aim to reduce crop damages (pers. obs.).

We studied wild boar range expansion from the Ardenne region, northwards across the Fagne-Famenne, Condroz and Loamy regions ($50^{\circ}25'N$, $4^{\circ}53'E$; Fig. 1). This area presents a south-north gradient in forest and agriculture cover, from highly forested (>75% of forest cover) in the southern Ardenne region to highly agricultural in the northern Loamy region (>75% of agricultural cover; SPW, 2012). Climate in the area is sub-oceanic, with mean annual temperature of $8^{\circ}C$, mean annual rainfall of 900 mm, and 25 days snow cover on average. Elevation ranges from 50 to 500 m. a.s.l.

2.2. Data sources

2.2.1. Wild boar presence data

We documented wild boar range expansion between 1981 and 2010 using questionnaire submitted to the different hunting territories located within the study area. In total, 382 game managers responsible for hunting territories (mean area 2.5 ± 2.0 (SD) km^2) participated to the survey. We questioned game managers on wild boar presence within their hunting ground. Specifically, we recorded periods of first wild boar appearance (i.e. sporadic presence), first wild boar shot, and periods from which they considered wild boar became permanently established in their hunting territory. We assumed game managers would recall about wild boar status over 5-year periods, and accordingly we segmented our study into six periods: 1981–1985, 1986–1990, 1991–1995, 1996–2000, 2001–2005, 2006–2010.

For each time step, survey information was geo-referenced into a 10×10 km grid resolution (Fig. 1), consistent with the fact that >96% wild boar have natal dispersal distance <10 km (Keuling et al., 2010; Prévot and Licoppe, 2013). For analysis, we only considered permanent presence of wild boar, since first appearances in unoccupied areas could result from the movement of solitary sub-adult individuals, and thus does not represent the overall population spread. When different periods were recorded among several hunting territories overlapping a same 10×10 km grid cell, we considered the earliest period of wild boar presence reported.

2.2.2. Colonization predictors

We explored the effects of seven variables to assess our four hypotheses of the colonization process of wild boar (Table 2). To assess the effect of natural landscape (first hypothesis), we calculated the 10×10 km grid cell 5-year mean percent of forest cover (FOREST). We extracted the data from the Belgium National Geographic Institute (NGI) vector map. To assess the effect of cultivated landscape (second hypothesis), we calculated the 5-year mean percent of crops providing cover to wild boar, i.e. maize *Zea mays*, rapeseed *Brassica napus* and cereals *Triticum* spp. (Brook and van Beest, 2014; Keuling et al., 2009). We lumped these different crops into one variable (AGRICOVER). Information on parcel cultivation was extracted and aggregated from data of the federal statistic (SPF Economie) for the period 1980–2000 and from the Walloon Public Service (SPW – SIGEC 'Système Intégré de Gestion et de Contrôle' – Agricultural land management map of Wallonia)

Table 1
Set of hypotheses and predictions driving the models development of wild boar range expansion in Southern Belgium, 1981–2010.

Hypothesis	Prediction	Interpretation
H1—Natural landscape	P1: Proportion of forest in unoccupied areas increase the likelihood of colonization	Recolonization
H2—Propagule pressure	P2: Presence of wild boar in the neighbourhood of unoccupied areas increase the likelihood of colonization	Invasion
H3—Cultivated landscape	P3: Crops providing cover (maize, wheat, rapeseed) in unoccupied areas increase the likelihood of colonization	Invasion
H4—Climate change	P4: Climatic change observed does not affect the likelihood of colonization, considering the spatial and temporal scales studied	Invasion

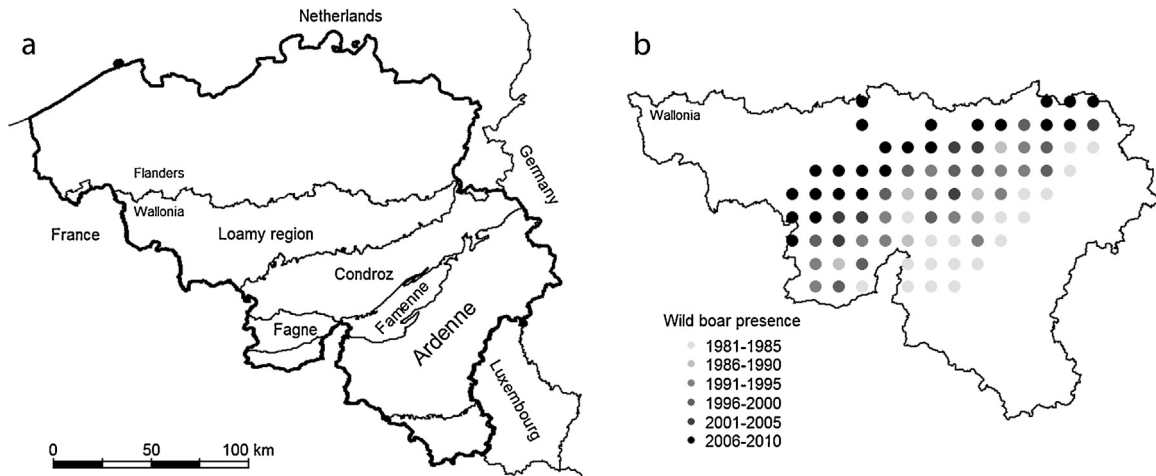


Fig. 1. (a) Belgium and the location of the different natural regions and (b) change in wild boar distribution (10×10 -km grid) between 1981 and 2010 in Wallonia, Southern Belgium.

for the period 2000–2010. To assess the level of propagule pressure (third hypothesis), we tested the effect of the number of the 8 adjacent cells occupied (Moore neighbourhood) on the probability of an empty grid to be colonized by wild boar (NGRID). We also measured the Euclidean distance to the closest occupied grid as a measure of the proximity to the population (PROX). To test the effect of climatic change (fourth hypothesis), we calculated 5-year mean annual temperature (TMEAN), mean temperature of the coldest month (TCOLD), and mean temperature of the warmest month in each cell (TWARM).

2.3. Data analysis

2.3.1. Range expansion pattern

Based on permanent wild boar presence data, we quantified the increase in occupied area across the whole study area by cumulating the newly occupied grid cells at each time period. We further estimated the velocity of expansion for each time period by calculating the barycentre (i.e. centroid) (i) of all occupied cells at each time step for the whole population expansion, and (ii) of the newly occupied cells for the expansion of the colonization front. We then calculated the distance and the direction between the different centroids ($t_{81-85} - t_{86-90}, t_{86-90} - t_{91-95}, \dots$). From the distances we could then estimate the mean population and front of expansion velocity by dividing the value by five (as one time period equal to five years). We calculated distance and direction parameters in R using the sp ([Bivand et al.,](#)

[2013](#); [Pebesma and Bivand, 2005](#)) and geosphere ([Hijmans, 2015](#)) packages.

2.3.2. Range expansion model

2.3.2.1. Dataset preparation. To reflect the expansion process of the wild boar population in Belgium over the last three decades, for each time period we (i) selected the newly colonized grid cells ('presence data') and the remaining uncolonized grid cells ('absence data') and (ii) excluded the grid cells colonized previously, which all remained occupied until the end of the study. For example, for the second period (1986–1990), we retained uncolonized and newly colonized grid cells compared to 1981–1985, i.e. excluding grid cells already colonized in 1981–1985. Doing so, presence–absence data at each time-step do not reflect the cumulative distribution of the species over time, but the incremental expansion into newly occupied areas from one period to another ([Barros et al., 2015](#)). We obtained a final dataset composed of 341 negative (cells not colonized at a given time period) and 79 positive (cells colonized) responses.

We screened explanatory variables for collinearity using a threshold of $|r| = 0.5$. The three climatic variables showed high level of correlation. We retained mean annual temperature for analyses, because it is a commonly used variable to track animal range-shift under climatic change ([Chen et al., 2011](#)). PROX and NGRID variables were also collinear, and because we assumed NGRID better explain our propagule pressure hypothesis, we retained this

Table 2

Independent variables used for modeling the colonization of wild boar in Wallonia, Belgium, 1981–2010.

Variables names	Description	Unit
Cultivated landscapes AGRICOVER	5-year mean area of grid cell covered by the following crop types: maize <i>Zea mays</i> , rapeseed <i>Brassica napus</i> , cereals <i>Triticum</i> spp.	km ²
Natural landscape FOREST	Area of grid cell covered by forest	km ²
Propagule pressure NGRID	Number of occupied cells (0–8) out of the 8 neighbouring cells	
PROX	Shortest Euclidean distance to a grid cell already occupied by wild boar	km
Climate variables		
TMEAN	Mean annual temperature	°C
TCOLD	Mean temperature of the coldest month	°C
TWARM	Mean temperature of the warmest month	°C

variable and excluded the variable PROX from the dataset. To confirm that collinearity was no longer an issue in our dataset, we calculated the variance inflation factors (VIFs) on a generalised linear model with binomial response (presence/absence) and a logit link function including all remaining variables. All VIF values were <10 which insured removal of collinearity (Neter, 1996).

To assess levels of spatial auto-correlation in the dataset, we fitted a generalized linear model with binomial response (presence/absence) and logit link function (logistic regression) including all variables (Hosmer et al., 2013; McCullagh and Nelder, 1989). We analysed the spline correlogram of the Pearson residuals. This analysis indicated no significant spatial auto-correlation at short and long distances.

2.3.2.2. Model selection. We modeled the probability of a grid cell to be colonized by wild boar between 1981 and 2010. We used presence/absence of wild boar in a grid cell as the response variable in a logistic regression model, and the variables representing our four hypotheses as explanatory variables. To explore the contribution of our four hypotheses on the range expansion of wild boar, we built a set of 15 *a priori* alternative models including all additive combinations of the explanatory hypotheses, a 'full' model fitted with all the variables, as well as a 'null' model with no explanatory variables (Table 3). To account for pseudoreplication due to grid cells repeatedly sampled over time, we fitted grid cell ID as a random intercept using a generalized linear mixed effects model (GLMM) approach (McCulloch et al., 2001). As fixed-effects, we used standardized explanatory variables to fit the models, in order to ease comparison of effect sizes.

We used an information theoretic approach to select for the most parsimonious model based on model selection criterion corrected for small sample size (AICc) (Burnham and Anderson, 2004). We performed model averaging of candidate models with cumulative weight <95% to estimate unbiased fixed-effect coefficients of the parameters. Coefficients were deemed significant in the final model when corresponding 95% confidence interval (CI) did not include zero. All analyses were run in R 3.2.0 (R Core Team 2013) and we used the lme4 (Bates et al., 2015), MuMIn (Barton, 2015) and AICcmodavg (Mazerolle, 2015) packages.

3. Results

3.1. Range expansion pattern

During the study period, the area occupied by wild boar increased by 7900 km² northwards (Fig. 1), corresponding to a

mean annual expansion rate of 266 km² year⁻¹. Though this rate was relatively constant between 1985 and 2005, we observed a slightly faster expansion during the first (1981–1985 with 380 km² year⁻¹) and the last phases of the study (2006–2010 with 480 km² year⁻¹), suggesting a three-phases expansion process (Fig. 2). Mean annual population velocity was 0.9 km year⁻¹ (range: 0.4–1.6 km year⁻¹) over the entire study period while the velocity of the front of expansion was 2.5 km year⁻¹ (range: 0.5–4.6 km year⁻¹). For both the population and the front of expansion, the orientation of the spread was Northwest to Northwest by North.

3.2. Range expansion model

From the fifteen alternative models tested, model 12 combining forest cover, number of neighbouring cells occupied, and mean annual temperature ranked as the most parsimonious model (Table 4). This indicates the combined role of three hypotheses in the expansion of wild boar in Belgium: natural habitat, propagule pressure, and climatic change.

Model-averaged fixed-effect coefficients indicate that wild boar colonisation probability of empty cells over the 30-year study period was positively associated to the number of neighbouring occupied grid cells ($\beta_{\text{NGRID}} = 0.692$, SE = 0.142, standardized 95% CI 0.414–0.974), forest cover ($\beta_{\text{FOREST}} = 0.468$, SE: 0.195, standardized 95% CI 0.052–0.847), and mean annual temperature ($\beta_{\text{TMEAN}} = 0.410$, SE = 0.170, standardized 95% CI 0.074–0.743) (Table 5). The strength of these variables on the expansion was however relatively different with the expansion being mostly influenced by neighbouring occupied grid cells, followed by forest cover and mean annual temperature (Fig. 3). Although the variable agricultural cover ($\beta_{\text{AGRICOVER}} = -0.021$, SE = 0.089, standardized 95% CI -0.378 to 0.213) was not informative in the final model, i.e. did not affect the expansion process, we observed that in the newly occupied areas by wild boar, agricultural cover increased at the expand of forest cover during the expansion process (Fig. 4).

4. Discussion

We studied the expansion of wild boar into Southern Belgian agroecosystems between 1981 and 2010, and assessed the contribution of four hypothesized mechanisms in influencing this process. We show that the expansion of the wild boar was a gradual, diffusive process driven by the combined effects of propagule pressure (i.e. number of occupied neighbouring cells), natural landscape availability (i.e. forest cover) and favourable climatic conditions (i.e. mean annual temperature). We found no support for changes in agricultural practices over the three decades

Table 3
Description of the tested hypothesis and the related model structure.

Model no.	Hypothesis	Model structure (fixed-effects)
0	Null	β_0
1	Natural landscape	$\beta_0 + \beta_1(\text{FOREST})$
2	Propagule pressure	$\beta_0 + \beta_1(\text{NGRID})$
3	Cultivated landscape	$\beta_0 + \beta_1(\text{AGRICOVER})$
4	Climate hypothesis	$\beta_0 + \beta_1(\text{TMEAN})$
5	Natural, propagule	$\beta_0 + \beta_1(\text{FOREST}) + \beta_2(\text{NGRID})$
6	Natural, cultivated	$\beta_0 + \beta_1(\text{FOREST}) + \beta_2(\text{AGRICOVER})$
7	Natural, climate	$\beta_0 + \beta_1(\text{FOREST}) + \beta_2(\text{TMEAN})$
8	Propagule, cultivated	$\beta_0 + \beta_1(\text{NGRID}) + \beta_2(\text{AGRICOVER})$
9	Propagule, climate	$\beta_0 + \beta_1(\text{NGRID}) + \beta_2(\text{TMEAN})$
10	Cultivated, climate	$\beta_0 + \beta_1(\text{AGRICOVER}) + \beta_2(\text{TMEAN})$
11	Natural, propagule, cultivated	$\beta_0 + \beta_1(\text{FOREST}) + \beta_2(\text{NGRID}) + \beta_3(\text{AGRICOVER})$
12	Natural, propagule, climate	$\beta_0 + \beta_1(\text{FOREST}) + \beta_2(\text{NGRID}) + \beta_3(\text{TMEAN})$
13	Natural, cultivated, climate	$\beta_0 + \beta_1(\text{FOREST}) + \beta_2(\text{AGRICOVER}) + \beta_3(\text{TMEAN})$
14	Propagule, cultivated, climate	$\beta_0 + \beta_1(\text{NGRID}) + \beta_2(\text{AGRICOVER}) + \beta_3(\text{TMEAN})$
15	Full	$\beta_0 + \beta_1(\text{FOREST}) + \beta_2(\text{NGRID}) + \beta_3(\text{AGRICOVER}) + \beta_4(\text{TMEAN})$

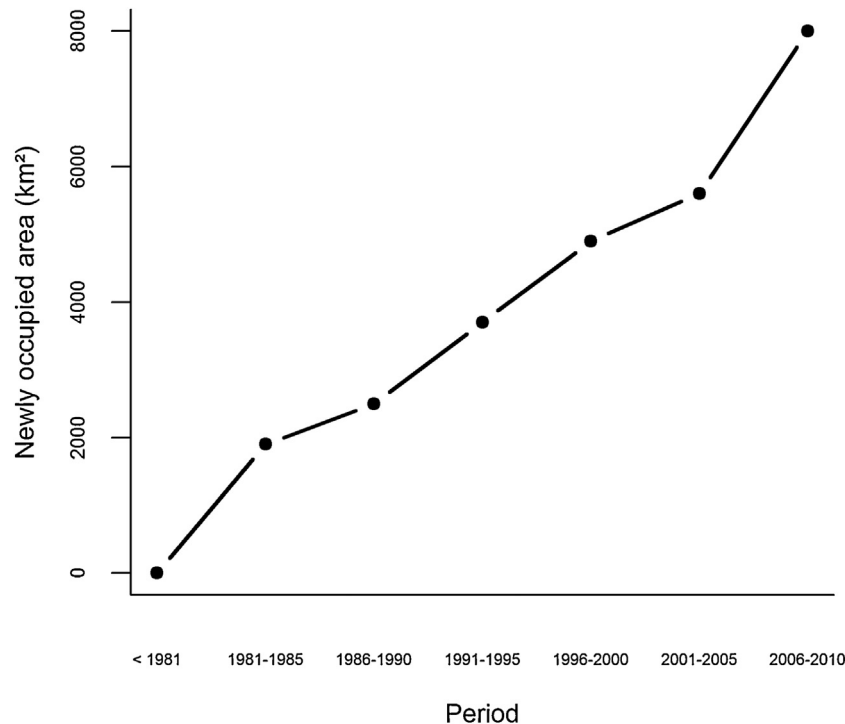


Fig. 2. Cumulative range increase of wild boar in Southern Belgium between 1981 and 2010.

Table 4

Model selection based on AICc. Model numbers correspond to numbers in Table 3.

Model number	K	AICc	Delta AICc	Modellik	AICcWt	LL	Cum. Wt
12	6	350.298	0.000	1.000	0.599	−169.047	0.599
15	7	352.068	1.770	0.413	0.247	−168.898	0.846
5	5	354.450	4.153	0.125	0.075	−172.153	0.921
11	6	355.609	5.312	0.070	0.042	−171.703	0.963
8	4	357.889	7.591	0.022	0.013	−174.896	0.976
2	3	358.266	7.968	0.019	0.011	−176.104	0.987
14	5	359.230	8.932	0.011	0.007	−174.542	0.994
9	4	359.606	9.308	0.010	0.006	−175.755	1.000
7	5	372.993	22.696	0.000	0.000	−181.424	1.000
13	6	375.052	24.754	0.000	0.000	−181.424	1.000
1	4	379.238	28.940	0.000	0.000	−185.571	1.000
6	5	380.987	30.689	0.000	0.000	−185.421	1.000
3	3	410.202	59.904	0.000	0.000	−202.072	1.000
10	4	411.444	61.146	0.000	0.000	−201.674	1.000
0	2	413.035	62.738	0.000	0.000	−204.503	1.000
4	3	414.340	64.042	0.000	0.000	−204.141	1.000

of the study to be a significant driver of wild boar range expansion in this landscape.

Despite being a relatively steady, low velocity diffusive process, wild boar spread in Belgian agroecosystems was dependent on the presence of the species in the neighbourhood of unoccupied areas, congruent with propagule pressure driving invasion (Table 1). Given the lack of detailed information on wild boar population density, we assumed that elevated neighbouring occupancy reflected higher surrounding density (Gaston et al., 2000). A positive relationship between neighbouring presence or density, and colonization probability is found in many other taxonomic groups (Lawton, 1993), and in terrestrial mammals in particular (Acevedo et al., 2005; Clobert et al., 2012). To our knowledge, the present study is the first to document this pattern in wild boar.

Diffusion process occurs when population-scale dispersal arise from dispersing individuals that remain in contact with the population along the front of expansion (Okubo and Levin, 2001), a

pattern also observed in wild boar (Cousse et al., 1994). The relatively low velocity we observed suggests that the colonization of Belgian agroecosystems by wild boar was predominantly the result of individuals dispersing over short distances, or home range drifts, rather than leapfrog long-distance dispersal events.

Table 5

Model-averaged fixed-effect coefficients (β), standard error (SE), and 95% confidence interval of variables explaining wild boar colonization in Southern Belgium, 1981–2010. Bold face indicates coefficients deemed significant in the final model as the 95% CI does not overlap zero.

	β	SE	95% CI lower	95% CI upper
(Intercept)	−1.727	0.153	−2.024	−1.423
FOREST	0.575	0.179	0.190	0.922
TMEAN	0.396	0.168	0.066	0.726
NGRID	0.667	0.140	0.393	0.943
AGRICOVER	−0.081	0.151	−0.377	0.216

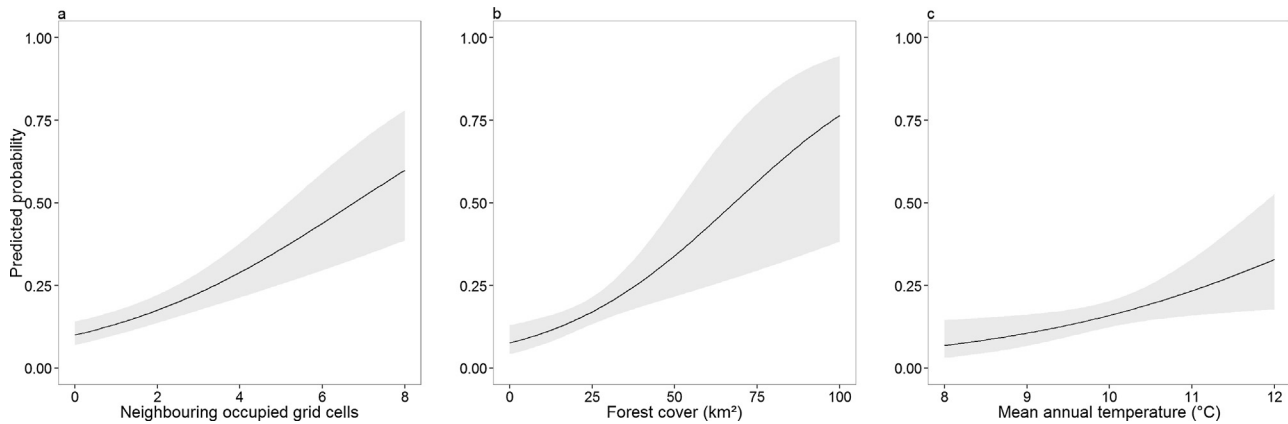


Fig. 3. Effect of significant variables on wild boar colonization probability in Belgian agroecosystems between 1981 and 2010.

Moreover, in our study, the annual expansion at the front of colonization (2.5 km) was similar to average female natal dispersal distance observed in Southern Belgium (Prévoit and Licoppe, 2013). This suggests that the expansion process is controlled by females (enabling reproduction and population establishment) rather than males (despite their greater dispersal capacity; see Prévoit and Licoppe, 2013), and that this phenomenon was appropriately captured by the use of permanent occupancy of wild boar as presence data in our model. Previous studies documenting wild boar spread observed expansion velocities much higher than in our study; ranging from 5 to 500 km year⁻¹ (Danilkin, 2001; Truvé, 2004). However, in both studies wild boar expansion was facilitated by intentional release away from the population margin, or escaped from farms, suggesting that wild boar spread in agroecosystems is natural, i.e. driven by natural dispersal from neighbouring areas and occurring via forest habitat.

In Western Europe, hunting contributes the most to wild boar mortality (Apollonio et al., 2010; Keuling et al., 2013). However, over the last decades, a decrease in the number of hunters has led to poor management efficiency, and to difficulties to control animal populations in agroecosystems (Cromsigt et al., 2013). This has played an important role in the increase of ungulates

populations throughout Europe (Massei et al., 2015; Milner et al., 2006) and Northern America (Riley et al., 2003). It is therefore likely that wild boar in Southern Belgium as in the rest of Europe benefited from a lack of top-down control, as release from predation or harvest can favour demographic recovery of populations and, through density-dependent dispersal, re-colonization of former range (Carey et al., 2012; Fattebert et al., 2015). Population density is also likely influenced by favourable climatic conditions increasing winter survival (Melis et al., 2006) and food availability throughout the year (Bieber and Ruf, 2005). This ultimately promotes population growth (Vetter et al., 2015), and sustain propagule pressure.

Contrary to our prediction, we observed a positive influence of higher mean annual temperature on the probability of colonization of unoccupied grid cells by wild boar. The significant role of the mean annual temperature variable in our modelling approach must however be carefully interpreted, considering the implication that the Northwestern expansion has on the altitudinal parameters. Indeed while moving from the Ardennes region, presenting altitudes above 400 m, towards Loamy plains, peaking at 100 m, wild boar simultaneously reach areas with milder and warmer mean weather conditions. This confounding effect of

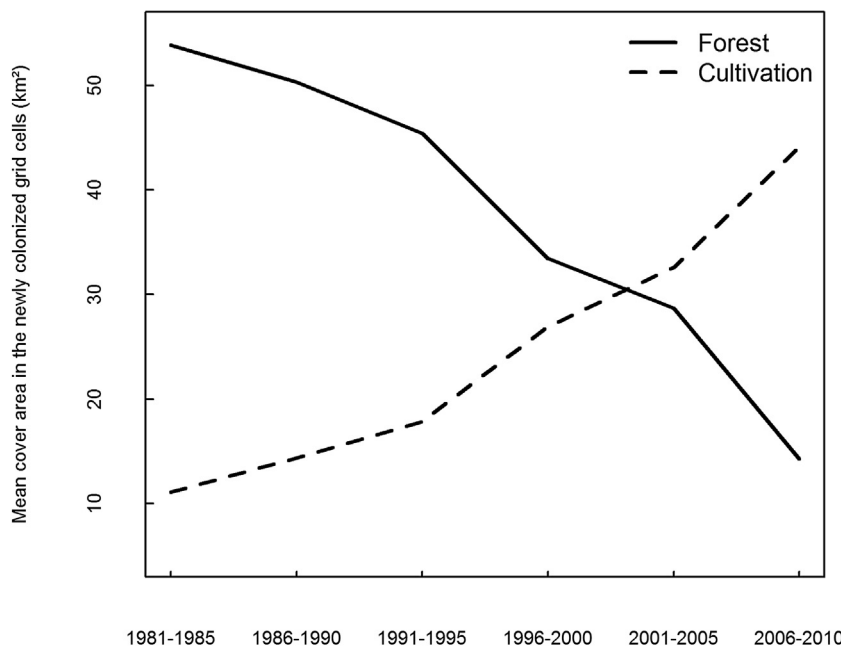


Fig. 4. Mean forest and cultivation cover area in grids newly occupied by wild boar during the colonization process.

altitude suggests that the role of climate should require further analysis over a broader scale, e.g. continental scale, to disentangle the effect of others factors (e.g. altitude, propagule pressure, land use change) from climate alone (Rosvold et al., 2013).

Finally, the importance of forest cover as a driver of wild boar range expansion supports our natural expansion hypothesis, and a simple re-colonization process. This is consistent with the role played by forest habitat documented at both coarse (Danilkin, 2001), and fine scales (Gerard et al., 1991). In agroecosystems, forest habitat, next to providing wild boar with food resources year-round and good protective cover, also constitutes an important corridor facilitating wild boar population movement. The positive effect of forest habitat on colonisation probability was therefore expected given the forest-dwelling nature of wild boar (Briedermann, 1990). Conversely, and contrary to our expectation, we found no support for the cultivated landscape hypothesis. Changes in the European agricultural policy in the 1980's promoting crops, e.g. maize *Z. mays*, potentially favourable to wild boar (van Vliet et al., 2015) did not directly influence range expansion. It is however likely that changes in food resources available in cultivated areas probably accelerated the phenomenon indirectly. Thanks to highly energetic seasonal food resources found in agricultural crops, fertility and population growth is indeed enhanced (Geisser and Reyer, 2005; Rosell et al., 2012), which consequently sustain the colonization/invasion process via propagule pressure.

Also, such a lack of effect of agricultural cover in wild boar colonisation might be due to the resolution of our analysis. At finer spatial scales, agricultural areas are increasingly used by wild boar (Keuling et al., 2009; Morelle and Lejeune, 2014), and wild boar home range and movement are influenced by agricultural landscape elements (Thurfjell et al., 2009). Our analysis at a coarse landscape scale likely highlights the hierarchical nature of habitat use and selection patterns, that differ across scales (Retting and Messier, 2000): while we demonstrate that the species still depends on forested areas to propagate at the population level, agricultural habitat may only play an important role at the individual level, and at the home-range scale. Nonetheless, we consider the spatial grain we used in the analysis offers the most consistent compromise between wild boar dispersal abilities and the hunter-based knowledge used to assess wild boar presence at a given time. This grid size also ensured that our results and their interpretation would refer to processes occurring at the population scale, and not at the individual scale.

Range expansion into agro-ecosystems has previously been documented in roe deer *Capreolus capreolus* (Acevedo et al., 2005), for which an agricultural ecotype has even been described (Hewison et al., 2001). Contrastingly, our results suggest wild boar might not yet demonstrate similar behavioural flexibility to roe deer in response to agroecosystems, and remain a forest-dwelling species. More intense hunting activities in agricultural areas to reduce risk of damages could explain a higher landscape of fear perception (Cromsigt et al., 2013; Tolon et al., 2009) towards this habitat in wild boar, consequently reducing the overall attractiveness of agricultural habitats, including for dispersal events.

5. Conclusions

While return or expansion of wild ungulates has been mostly associated to rural depopulation and land abandonment (Acevedo et al., 2010; Hearn et al., 2014), we documented for the first time expansion into a region characterized by an increasing rural demographic pressure (Thomsin, 2000). Previous studies on wild boar spatial dynamics in similar socio-economic contexts focused on the establishment of the species in peri-urban areas (Cahill and

Llimona, 2004; Licoppe et al., 2014), corresponding more to range-filling than to range expansion as documented in our study.

Our results demonstrate the steady, gradual colonization of the wild boar into Belgian agroecosystems. Wild boar distribution dynamics was driven by a combination of invasive (propagule pressure and climate change) and recolonization (natural landscape) mechanisms. The recolonization mechanism through forest habitat is consistent with the recovery of the wild boar in Europe since the second part of the 20th century (Deinet et al., 2013), but also suggests the species might be limited in its expansion by the availability of forest cover in similar landscapes elsewhere in Western Europe. The role played by invasive mechanisms corroborates the multiple traits that wild boar share with invasive species: early age at first reproduction (Servanty et al., 2009), high reproductive output (Servanty et al., 2009), generalist feeding strategy (Schley and Roper, 2003), spatial behavioural plasticity (Podgórski et al., 2013), and commensalism with humans (Cahill et al., 2012). Although the cultivated landscape was not an important driver of the colonization process, access to croplands and their high quality food resources that likely provide wild boar with a competitive advantage to spread in agroecosystems in an invasive-like fashion (Valéry et al., 2008). A process further enhanced by favourable climatic conditions. Further investigations on the spatial and demographic dynamics of wild boar in agroecosystems over a broader scale is however needed to improve our understanding of the complex interactions between the species' traits and anthropogenic (land use modifications, climate change) processes.

Based on our results, we suggest that future of wild boar management in agricultural landscapes should concentrate on the implementation of management strategies aiming at controlling the species expansion, e.g. reduce attractiveness of corridors (forest) by increasing the landscape of fear associated to this habitat and limit slow diffusion of the population in unoccupied areas. Our modelling approach could be applied to repeated survey data (Broms et al., 2016), to measure the effect of various control strategies on the spatial-temporal dynamics of wild boar population over large scale, providing a powerful tool for informing managers and adapting culling plans.

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