

# Catastrophic impact of wild boars: insufficient hunting pressure pushes snakes to the brink

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## Keywords

Extinction; habitat destruction; hunting pressure; predation; *Vipera*; wild boar; population control.

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## Abstract

Climatic changes, habitat loss and invasive species are important threats for many animal populations. Here, we report rapid declines and extinctions of adder populations monitored during 12 years in Belgium where none of the above causes was involved. This study provides the first large-scale data showing that wild boars represent a major risk for snakes, pushing populations to extinction. Drastic population declines were observed in the sites impacted by wild boars ( $N = 14$ ), while in other sites spared by wild boars populations remained stable ( $N = 9$ ). Wild boars are highly fertile and their main predators have been extirpated from Western Europe; yet, recreational hunting kept populations in check during decades. Hunting pressure is currently insufficient to control the rapid expansion of wild boars, demographic outbreaks are increasingly frequent. Wild boars are omnivorous; they can destroy snakes directly and indirectly through the depletion of snake's preys and via the destruction of key microhabitats. Snakes exhibit limited dispersal capacities; they cannot escape local perturbations and thus are highly vulnerable. Because wild boars have a very eclectic diet, are prolific breeders and are able to devastate a range of habitats their negative impact under relaxed hunting pressure applies to a huge variety of organisms, including reptiles. Policies to limit wild boar populations are urgently needed. Recommendations to target reproductive females and piglets should be generalized and applied.

## Introduction

The erosion of animal biodiversity pertains to a set of global causes. Climatic changes, loss and fragmentation of habitats, over exploitation of resources, alien species invasion, or the propagation of diseases can provoke population collapses (Clavero & García-Berthou, 2005; Smith, Sax & Lafferty, 2006; Ricciardi, 2007; Sinervo *et al.*, 2010; Ceballos *et al.*, 2015; McCauley *et al.*, 2015). These processes rarely function in isolation; instead, synergistic disruptions eventually lead to species extinction (Brook, Sodhi & Bradshaw, 2008). Yet, complex and paradoxical effects have been documented, for example in different ecosystems, introduced species contributed to the restoration of biodiversity through the stabilization of trophic networks (Wallach, Ripple & Carroll, 2015). In this multifactorial context, it is important to consider the interactions among species to accurately forecast possible consequences of global changes on populations. Monitoring general trends is equally important to promote public awareness and to influence conservation policies (Mace & Baillie, 2007). But it is also crucial to identify the threats that require urgent actions at a local scale.

One ungulate species is of major concerns in its wide native distribution range: the wild boar *Sus scrofa*. It shares peculiar life-history traits with highly invasive species. Wild boars display high reproductive capabilities and a short generation time compared to other similar-sized ungulates (Servanty *et al.*, 2011). They can adapt rapidly to novel environments, are opportunist, and thus can pullulate in the absence of predators (review in Ruiz-Fons, 2017). They have been categorized among the world's worst invasive organisms of the planet (Lowe *et al.*, 2000). In their original distribution range and in the places where they have been introduced they can threaten whole ecosystems due to their multi-target impacts (Barrios-Garcia & Ballari, 2012). They cause strong damages to soils, they eat and destroy a wide range of plants, invertebrates, vertebrates, and in addition they are vectors of diseases (Bueno *et al.*, 2011; Barrios-Garcia & Ballari, 2012; Bevins *et al.*, 2014; Murphy *et al.*, 2014; Parkes *et al.*, (2015); Wilcox, 2015). Wild boars deeply excavate or compact large surfaces, lifting stones, logs (e.g. rooting, wallowing) and destroying key habitats that are essential for ground dwelling organisms. Because they live in family groups (sounders), local impacts can be

extreme, even in their native distribution range (Ickes, Paciorek & Thomas, 2005).

Many reptiles exhibit cryptic lifestyle and cannot survive without shelters (thick herbaceous layers, shrubs, logs, burrows, stones, etc.); a dearth of refuges entails behavioral, physiological and demographic disorders (Lagarde *et al.*, 2012; Bonnet, Fizesan & Michel, 2013; Bourke, Matthews & Michael, 2017; Carpio *et al.*, 2017). Lizards, snakes and chelonians have been regularly found in the stomach of wild boars (Taylor & Hellgren, 1997; Fordham *et al.*, 2006; Jolley *et al.*, 2010; Wilcox, 2015). Finally, most terrestrial reptiles exhibit sedentary habits (Shine, 2005), and thus they have little options to escape demographic bursts of wild boars.

Reptiles face strong declines worldwide (Böhm *et al.*, 2013). Snakes that broadly contain one-third of reptilian species are heavily impacted (Zhou & Jiang, 2004; Santos & Llorente, 2009; Seigel & Mullin, 2009; Reading *et al.*, 2010). Many populations are now strongly fragmented (Luiselli & Capizzi, 1997; Row, Blouin-Demers & Lougheed, 2010; Meek, 2012). Thus, wild boars may deliver the coup de grâce to already fragile snake populations. The current study was not primarily designed to investigate the impact of wild boars on snakes. Instead a long-term survey program set up more than 12 years ago (2005) aimed to assess the ecological characteristics of 23 populations of adders *Vipera berus*, and to examine the influence of habitats and climate on different traits (Graitson, 2008, 2011). This study was framed into the global context of highly fragmented and threatened snake populations that prevails in Western Europe. Initially, one key objective of this study was to contribute to the protection of isolated populations of snakes. In practice, conservation actions for habitat management have been undertaken, notably to maintain open areas that are favorable to snakes (Graitson, 2011). Expectedly, newly opened areas should have promoted snake populations, a technique successfully tested in a comparable context (Bonnet *et al.*, 2016).

The sudden irruption of wild boars upset the initial plans and provided an (undesired) opportunity to compare impacted versus spared populations. This swift change of priority is typical of what is predicted in many places in the near future because wild boars exhibit a rapid demographic growth across their distribution range (Ruiz-Fons, 2017). The long-term monitoring of adder populations offers a solid background to examine a single question: are wild boars becoming the main menace for reptiles in Western Europe?

## Materials and methods

### Studied species

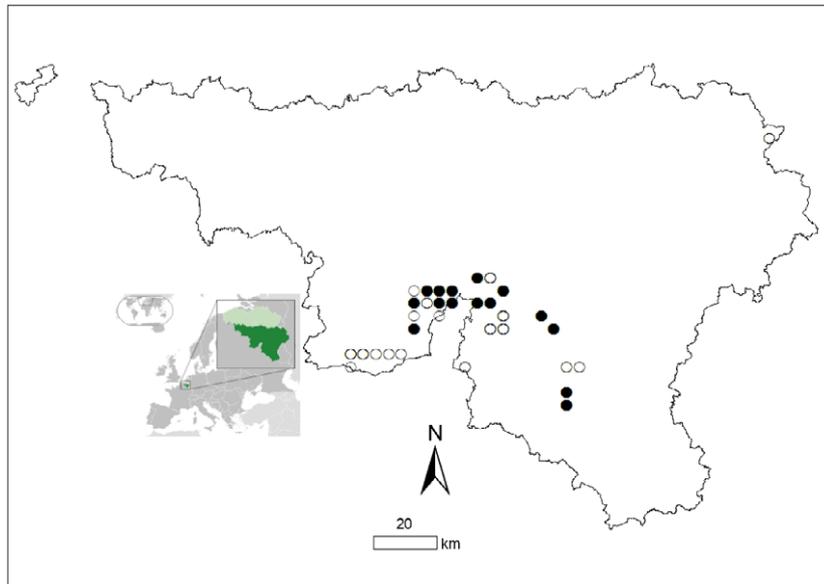
The adder *Vipera berus* is widely distributed in the Palaearctic. This snake occupies various habitats (hedgerows, forest clearings, meadows, moors, etc.). Habitat complexity is essential, notably open areas for sun basking in alternation with thermally buffered shelters and shrubs (Leibl & Völkl, 2009). These features are also important for the prey of the

adders. Adults feed mainly on micro-mammals and lizards, juveniles often consume amphibians (Luiselli & Anibaldi, 1991; Monney, 1996). This species displays limited dispersal abilities, pronounced site fidelity and slow demographic traits (Madsen & Shine, 1994; Phelps, 2004). Habitat fragmentation caused by the intensification of agricultural practices and urban sprawl induces genetic depression, especially in small isolated populations with potential deleterious effects (Madsen *et al.*, 1999, 2000; Ursenbacher, Monney & Fumagalli, 2009). This species is declining in countries that have been accurately monitored (Schiemenz, 1995; Reading *et al.*, 1996; Van Delft & Janssen, 2015). Although not yet categorized as threatened across its vast distribution range (a reassuring status mainly due to data deficiency) it is included in the red lists of most Western European countries, previously prosperous populations are now residual in many places (Monney & Meyer, 2005; Reading *et al.*, 2010).

### Study sites

Belgium is a country representative of densely populated hence highly urbanized areas (>3 million hectares, >11 million inhabitants). Remaining habitats favorable for snakes are patchy and concentrated in the south regions (e.g. 80% of forests are situated in Wallonia; Jacob *et al.*, 2007); an isolated and large population persists in northern Belgium in a military zone (Bauwens, Claus & Mergeay, 2018). From 2000, patches of suitable habitats were intensively prospected in southern Belgium in a landscape that broadly covers 300 000 hectares (49.85°N and 50.2°N, 4.6°E and 5.3°E, humid temperate climate, 70–500 m ASL, Fig. 1). A total of 23 sites were selected (Table 1). Other sites where adders have been observed since 2000 (usually only one snake observed despite multiple visits) were not retained due to the very low densities (Fig. 1). Each site was characterized by its surface (0.5–25.0 hectares), habitats (e.g. unmanaged meadows, hedgerows, forest clearings, moorlands, or railway embankments), and protection status (protected vs. unprotected, sometimes covered by Life Program actions).

Rooting is the most obvious sign of the presence of wild boars (Fagiani *et al.*, 2014), and counting individuals (e.g. during nocturnal transects) correlates with mark-recapture density estimates (Franzetti *et al.*, 2012). Thus, we used rooting intensity as a proxy for the presence/abundance of boars. At the beginning of the study (2005), rooting was either absent (code = 0), or limited (code = 1: less than 3% of the ground surface impacted annually). Broadly 5 years later (2009–2010), rooting increased in different sites, generating moderate (code = 2: 3–10%) to strong (code = 3: 11–80%) impacts on the ground surface. Once first recorded in a given site, rooting intensity never decreased, suggesting that constant or increasing numbers of wild boars foraged in the sites they selected. This generated a simple pattern: the impact of wild boars increased in some sites while it remained low (or null) in the others. We cannot exclude the fact that wild boars occasionally penetrated the presumably not-impacted sites without leaving any visible sign (e.g. no rooting, dropping, tracks). Therefore, we cannot ascertain



**Figure 1** Distribution of *Vipera berus* in southern Belgium. Black dots indicate the location of the 23 studies sites surveyed during 12 years; note that at this scale several sites are overlapping. White dots indicate locations where adders were seldom observed (very small populations). Adders concentrate in southern areas where natural habitats remain (e.g. forests, meadows). In these areas precisely, wild boar population are rapidly growing (Figure S1).

**Table 1** Main characteristics of the 23 sites where populations of adders *Vipera berus* were monitored from 2005 to 2016

Site #	WB-impact	Surface	Main habitat	Protection status	LIFE	AF	Other	Pop
S08	0	2	Hedgerows	Natura 2000	No	No		Stable
S11	0	1	Railway	None	No	No	Closing	Stable
S12	0	10	Shrub	Nature Reserve	No	No		Stable
S13	0	2	Shrub	Nature reserve	No	No		Stable
S21	0	1	Shrub	Natura 2000	No	No	Closing	Stable
S22	0	4	Railway	None	No	No		Stable
S23	0	1	Railway	None	No	No		Stable
S02	1	4	Shrub	Natura 2000	No	No		Stable
S03	1	0.5	Shrub	Nature reserve	No	No		Extinct
S18	1	2	Forest clearings	Natura 2000	No	No	Closing	Stable
S10	1	1	Railway	None	No	No		Decline
S01	2	5	Forest clearings	Nature Reserve	Yes + 5 ha	No		Decline
S04	2	1	Shrub	Natura 2000	No	No	Closing	Decline
S05	2	23	Hedgerows	Natura 2000	Yes	No	Agr +	Decline
S07	2	12	Shrub	Natura 2000	No	No	Closing	Decline
S09	2	0.5	Forest clearings	None	No	Yes		Decline
S06	2	2	Forest clearings	Nature reserve	Yes + 1 ha	No		Extinct
S14	2	6	Hedgerows	None	Yes	No		Extinct
S15	2	4	Hedgerows	Natura 2000	Yes + 1 ha	No		Extinct
S16	2	0.5	Forest clearings	None	Yes + 2 ha	Yes		Extinct
S17	2	1	Forest clearings	None	Yes + 3 ha	Yes		Extinct
S19	2	7	Hedgerows	Natura 2000	Yes + 4 ha	No		Extinct
S20	2	10	Hedgerows	None	No	No	Agr +	Extinct

The first column indicates site number. WB-impact stands for wild boar impact (0 = low, 1 = moderate, 2 = severe, see text). Surface is expressed in hectares. Main habitat indicates major microhabitats used by the adders (e.g. railway means that the snakes were often observed basking on/or near the railway embankment). LIFE indicates if the site benefited from LIFE actions for reptiles and amphibians (extension around main site: + n ha). AF means artificial wild boar feeding. Closing means habitat closure due to forest growth, Agr+ means agricultural intensification. The last column (Pop) indicates the change in population status from the onset of the study to 2016 (see text and fig. 4).

that a given site was never impacted at all. Consequently, we classified the sites into three groups (Table 1): (1) in seven sites the presence of boars, if any, was minimal during the whole study (e.g. rooting code = 0 in four sites and 1 in three; without change over time); (2) in four sites we recorded a moderate albeit increasing presence of boars (rooting code changed from 1 [three sites] or 0 [one site] to reach 2 in all cases); (3) twelve sites were heavily impacted (rooting code changed from 1 to 3 in all cases). Henceforth, considering the marked differences in changes of rooting intensity over time, the three types of sites were named as follow: low impact sites ( $N = 7$ ), moderate impact sites ( $N = 4$ ), and severe impact sites ( $N = 12$ ).

At the onset of the study, we found no significant difference between protected versus not-protected sites, or impacted versus not-impacted sites, in terms of surface or in terms of adder-counts (Kruskal–Wallis ANOVAS, all  $P > 0.08$ ; Table 2). Although not significantly (due to large confidence intervals), protected sites tended to be larger, to initially shelter a greater number of adders, but they became the most severely impacted.

### Snake population monitoring

Between 2005 and 2016 (12 years), standard visual transects (SVT) were performed by EG with nine volunteers. EG performed the majority (>50%) of the surveys and visited all the sites during the entire period. The number of visits varied between years (range 29–166) and increased over years ( $r = 0.64$ ,  $P = 0.025$ ). All field workers were well-trained and adders are easily spotted when basking in the field. Adders were searched and counted during the active season (March to September) when snakes were the most likely to bask under the sun. Evidences of adder presence were also taken into account (e.g. sloughed skin) when no snake was visible. On average, the sites were visited 46.1 times for a total of 1061 SVT (15–111 SVT per site, ~4.7 per year on average).

Adders are sedentary animals; variations in visual counts reflect changes of population density (Madsen & Ujvari, 2011). In each site and each year, we recorded mean and maximal numbers of adders sighted. Mean adder-count was calculated as the mean number of adders sighted; max adder-count indicates the highest number of adders sighted during a SVT (best SVT score). During a given SVT a single route was patrolled only once; individuals were not counted more than once. The annual detectability of adders is less than 1, even under intensive monitoring (Bonnet & Naulleau, 1996). Thus, adder-counts provided values that underestimated population size. Individuals not observed during three consecutive years are considered dead (Bonnet *et al.*, 2002), thus the total lack of snakes in a site during four consecutive years meant that the population was extinct or close to extinction.

### Analyses

Because snake detectability can be relatively low (e.g. under unfavorable climatic conditions), we used site occupancy analyses to assess the impact of wild boars on the probability to detect adders (MacKenzie *et al.*, 2003). The 23 sites were not all surveyed every year. From a theoretical number of 276 mean adder-counts (23 sites  $\times$  12 years), 50 were missing (~18%). The number of missing adder-counts ranged from 0 to 10 among years with an average annual value of  $4.17 \pm 3.04$  ( $\pm$ SD), and ranged from 0 to 6 among sites with an average value of  $2.13 \pm 1.96$ . Missing adder-counts concerned the three categories of sites: 21% in the low impact sites, 23% in the moderate impact sites, and 15% in the severe impact sites, without significant difference among them (Kruskal–Wallis ANOVA,  $H = 2.579$ ,  $P = 0.276$ ). Yet, each site was surveyed most years and most sites were surveyed several times per year (4.7 SVT/site/year on average), enabled us to build the occupancy history of the 23 sites.

Some sites were surveyed more than 10 times certain years (range: 11–26); in these cases we merged consecutive

**Table 2** Comparison of important features (means  $\pm$  sd) of the sites monitored at the onset of the study (2005), with respect to their protection status, the occurrence of LIFE program actions, and in function of future wild boar impact level (WB0 – WB2), see table 1 for details: surface (ha), initial searching effort (number of standard visual transects, Ini-SVT), initial mean adder counts (number of adder/SVT, Ini-adder), initial maximal numbers of adders (best SVT, Ini-Max adder), total number of SVT during 12 years (SVT-12), number of years surveyed (Years monitored, Y-M)

Source	Surface	Ini-SVT	Ini-adder	Ini-Max adder	SVT-12	Y-M
Protected	5.4 $\pm$ 6.1	4.9 $\pm$ 2.7	3.0 $\pm$ 3.4	13.1 $\pm$ 17.3	54.6 $\pm$ 33.4	11.3 $\pm$ 1.6
Not Protected	2.8 $\pm$ 3.3	3.0 $\pm$ 1.4	1.4 $\pm$ 2.0	3.2 $\pm$ 4.6	32.9 $\pm$ 16.6	10.9 $\pm$ 2.0
Ratio	1.9	1.6	<b>2.1</b>	<b>4.1</b>	1.7	1.0
LIFE	6.1 $\pm$ 7.2	3.0 $\pm$ 3.0	4.5 $\pm$ 8.4	12.6 $\pm$ 21.0	43.3 $\pm$ 36.4	11.9 $\pm$ 0.4
No LIFE	3.5 $\pm$ 3.9	3.3 $\pm$ 3.7	2.4 $\pm$ 2.6	7.5 $\pm$ 9.8	47.7 $\pm$ 26.7	10.7 $\pm$ 2.1
Ratio	1.7	1.0	1.9	1.7	0.9	1.1
WB 0	3.0 $\pm$ 3.3	2.1 $\pm$ 3.6	1.9 $\pm$ 2.1	5.4 $\pm$ 9.8	54.4 $\pm$ 23.7	10.9 $\pm$ 2.2
WB 1	1.9 $\pm$ 1.5	3.0 $\pm$ 2.9	1.5 $\pm$ 1.3	4.0 $\pm$ 3.7	29.8 $\pm$ 16.2	10.5 $\pm$ 1.9
WB 2	6.0 $\pm$ 6.6	3.9 $\pm$ 3.4	4.4 $\pm$ 7.0	13.3 $\pm$ 18.0	46.8 $\pm$ 35.2	11.5 $\pm$ 1.4
Ratio	<b>4.1</b>	1.9	<b>2.9</b>	<b>3.3</b>	1.8	1.1

None of the comparison lead to significant difference (all  $P > 0.08$ ). Ratios facilitate the visualization of differences between extreme values (ratios>2 are in bold).

SVT into a single capture session to limit heterogeneity in occupancy histories between sites and the weight of missing data (the maximal number of SVT per year per site was limited to 10). Overall, the final matrix used for site occupancy analyses was based on 605 surveys from 1061 initially available. For simplicity, we coded adder occurrence in each site dichotomously: 0 (absent) and 1 (present). We thus ignored the actual numbers of adders sighted during SVT (ranging from 0 to 26 adders per SVT, a total of 1879 adder observations was collected during the study).

Multi-season site occupancy statistical models use detection-nondetection data from a sample of locations monitored during consecutive years in order to estimate the probability a given site to be occupied by a species of interest, as well as dynamic parameters which are local extinction probability and colonization probability (MacKenzie *et al.*, 2003). These models were specifically designed to estimate these probabilities when a species is not detected with certainty. We used robust design occupancy models with relaxed closure (Kendall *et al.*, 2013). These models are based on the collection of multiple samples at each of a number of sites within a given season, and permit staggered entry and exit times for the species at each site. We suspected models with relaxed closure would better fit to the data since the within season sampling period extended from March to September, therefore allowing individuals to move within or outside sampled transects. Moreover, adder detectability varies during season due to varying thermal requirement, sex and reproductive status (Bonnet & Naulleau, 1996).

The occupancy history dataset consisted of 12 primary periods covering 12 years. Within each primary period, there were multiple secondary sampling periods (from three to ten). Our starting model included six parameters (Table S1). To model the effect of the presence of wild boars on the adder population dynamics, all parameters were set group-specific. Due to the relatively small number of sites, we had to constrain some parameters to make them estimable. Extinction and colonization probabilities were group, but not season dependent. Entry, departure and detection probabilities varied between groups and seasons, that is, they were not allowed to vary between sampling occasions within seasons. From this starting model we tested for possible effects of season and group on detection, departure and entry probabilities. Once the best model structure was identified for these parameters, we tested for group effects on extinction and colonization probabilities.

Model fitting and parameter estimation were performed using a Bayesian approach using Markov chain Monte Carlo (MCMC) simulation implemented in program MARK (White & Burnham, 1999). For model fitting, we ran 15 000 iterations with an initial burn-in of 4000 iterations and a tuning of 1000 iterations. We ran two chains to obtain a diagnostic value (R-hat) useful for determining if the Markov chains adequately sampled the posterior distribution (i.e. R-hat  $\approx$  1). Model selection was performed using the Watanabe-Akaike information criterion (WAIC, Watanabe, 2010).

However, in the site occupancy analysis the presence of a single adder in a given site was coded 1, the same code was

used when large numbers of snakes were observed (e.g. highest max adder-count was 26, a value that underestimated actual population size). Consequently, crucial information about possible snake decline over time was lost. Mean adder-counts provided values averaging the counts performed each year. They strongly underestimated snake population size but they nonetheless retained an important amount of variance. Therefore, we also provide the results from mean adder-counts as a mean to visualize population trends (Appendix S1).

Analyses were performed with MARK and STA-TISTICA.13 software (Dell Inc. (2015). Dell Statistica, version 13. software.dell.com.).

## Results

Mean annual searching effort (number of SVT/year) significantly increased over years while mean annual adder-count significantly decreased (Fig. 2). Thus, despite increased searching effort fewer adders were sighted over time.

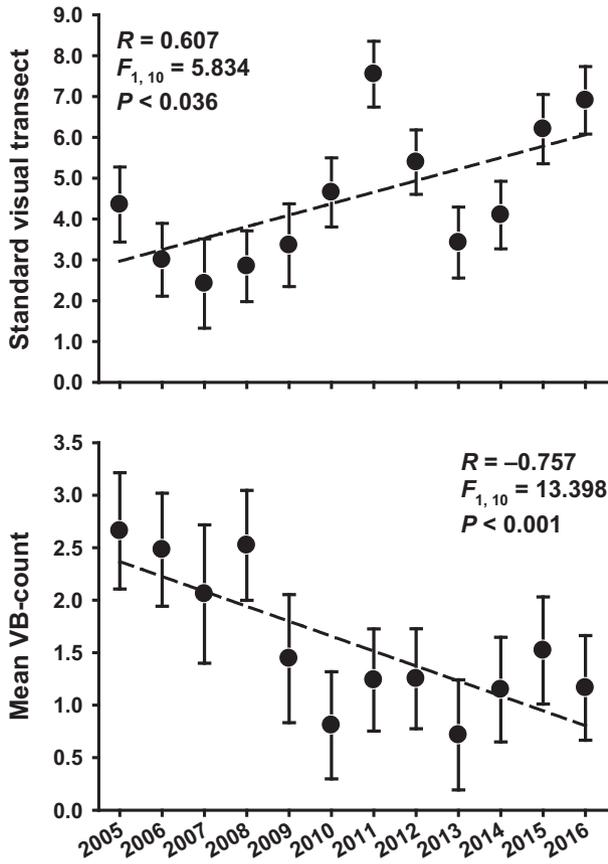
### Site occupancy analyses

All models converged adequately (R-hat  $\approx$  1). Model selection statistics provided strong evidence for lack of closure since entry and departure probabilities varied between years and groups (M2 vs. M5, M6, Table 3). Entry probabilities varied between 0.193 in group 3 in 2014 to 0.931 in group 3 in 2012, and departure probabilities varied between 0.050 in group 1 in 2016 to 0.639 in group 2 in 2015 (Table 4). Model selection also indicated that detection probability varied between groups but not between years (model M2 vs. M1, M3, M4, Table 3). There strong evidence that extinction probability and colonization probabilities varied between groups (M2 vs. M7, M8, Table 4). Extinction probability was lower in group 1 (WB 0) than in group 2 (WB 1) and 3 (WB 2), and colonization probability was lower in group 3 than in group 1 and 2 (Table 4). As a result occupancy probabilities decreased in groups 2 and 3 but remained stable in group 1 (Fig. 3).

### Mean adder-counts

The effect of wild boars on adder-counts was strong (Fig. 4, Appendix S1). At the beginning of the study, mean adder-counts from low impact sites and from severe impact sites were similar, and remained relatively similar until 2008 (se largely overlapping). The strong decline observed in severe impact sites between 2008 and 2010 contrasted with stability of low impact sites. Then, the continuous decline of mean adder-counts in severe impact sites versus stability in low impact sites eventually lead to stable populations versus strongly reduced or extinct populations. In moderate impact sites, mean adder-counts were initially lower compared to the other groups, they nonetheless decreased over time and exhibited very low values after 2009.

In order to appraise the main changes of population status during the 12 years of the study, we compared the mean adder-counts of the first three years (2005–2007) with the



**Figure 2** Changes in searching effort (mean number of SVT, standard visual transects) and adder-counts (mean number of adder observed per SVT) during 12 years ( $\pm$ sd). Searching effort increased over time while mean adder-counts dropped, notably in 2009 without subsequent recovery despite important searching effort (e.g. 2011).

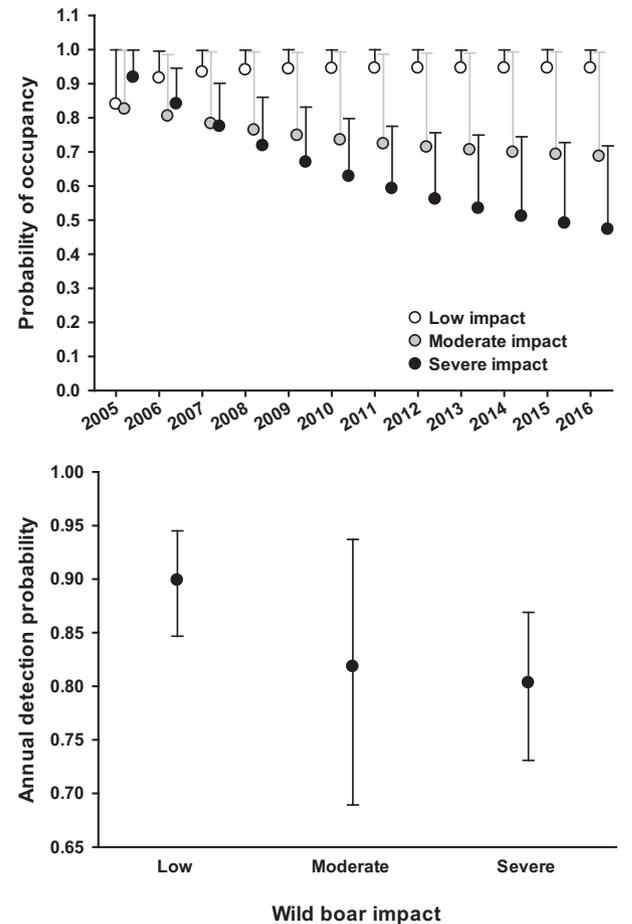
**Table 3** Modelling the effects of year and group on probabilities of detection ( $p$ ), departure ( $d$ ), entry ( $\beta$ ), colonization ( $\gamma$ ) and extinction ( $\epsilon$ ) of adders on 23 sites in southern Belgium between 2005 and 2016

Model	Notation	Hypothesis	WAIC
M1	$\psi_{g\epsilon g} \gamma_g \beta_{g,t} d_{g,t} p_{g,t}$	-	629.4
<b>M2</b>	$\psi_{g\epsilon g} \gamma_g \beta_{g,t} d_{g,t} p_g$	<b>No year effect on detection</b>	<b>625.7</b>
M3	$\psi_{g\epsilon g} \gamma_g \beta_{g,t} d_{g,t} p_t$	No group effect on detection	629.9
M4	$\psi_{g\epsilon g} \gamma_g \beta_{g,t} d_{g,t} p$	Constant detection	633.4
M5	$\psi_{g\epsilon g} \gamma_g \beta_g d_g p_g$	No time effect on entry and departure	805.8
M6	$\psi_{g\epsilon g} \gamma_g \beta_t d_t p_{g,t}$	No group effect on entry and departure	686.3
M7	$\psi_{g\epsilon} \gamma_g \beta_{g,t} d_{g,t} p_g$	No group effect on extinction	636.2
M8	$\psi_{g\epsilon g} \gamma_g \beta_{g,t} d_{g,t} p_g$	No group effect of colonization	628.8

$g$  indicates the wild boar group effect (low, moderate and severe impact),  $t$  indicates year, WAIC : Watanabe-Akaike information criterion. The model selected is indicated in bold.

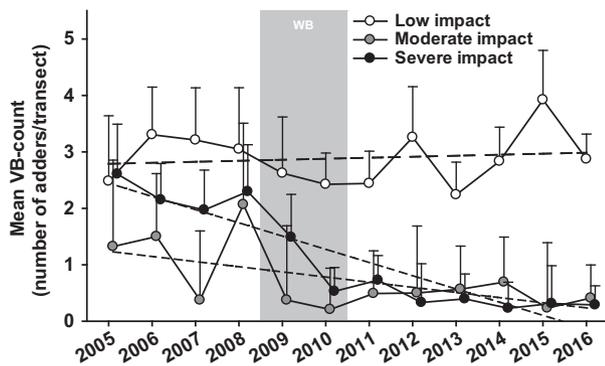
**Table 4** Estimates, standard errors (SE) and 95% highest posterior density (HPD) intervals of parameters estimated under the selected model (M2, Table 3) for the three groups of sites regarding the impact of wild boars (1: WB0, 2: WB1, 3: WB2)

Parameter	Estimate	SE	95% HPD interval
$\psi_1$	0.840	0.134	0.565–0.999
$\psi_2$	0.825	0.142	0.527–0.997
$\psi_3$	0.918	0.067	0.781–0.998
$\epsilon_1$	0.025	0.019	0.009–0.061
$\epsilon_2$	0.067	0.045	0.005–0.153
$\epsilon_3$	0.089	0.028	0.036–0.143
$\gamma_1$	0.585	0.275	0.093–0.994
$\gamma_2$	0.191	0.207	0.004–0.712
$\gamma_3$	0.052	0.042	0.009–0.137



**Figure 3** Changes in estimated occupancy probabilities of 23 sites by adders through time (12 years) in function of the impact level of wild boars: low impact sites ( $N = 7$ ), moderate impact sites ( $N = 4$ ) and severely impact sites ( $N = 12$ ) (Top panel). Detection probability of adders in function of the impact level of wild boars (Bottom panel). Mean values are shown  $\pm 1$  SE.

last 3 years (2014–2016). Six years elapsed between the two periods, and few adders (likely none in most populations) were represented in both. In low impact sites, initial 3y-



**Figure 4** Impact of wild boars on mean adder-counts ( $\pm$ SE) from 2005 to 2012. In low impact sites (white circles,  $N = 7$ ), rooting remained minimal (0%–<rooting<3% of the ground surface) and mean adder-count were relatively stable. In severely impacted sites (black circles,  $N = 12$ ), rooting was minimal during the 4 years of the study but suddenly increased in 2009 without subsequent decrease (~11% to 80% of the ground surface). A concomitant collapse of adder-counts was observed. In moderately impacted sites (grey circles,  $N = 4$ ), initial adder-counts were relatively low. Rooting increased in 2008–2010 (3–10% of the ground surface) and adder-counts then decreased. Dashed lines show linear regressions. The grey area (WB) indicates the period during which wild boars started to use (intensively) impacted studied sites. Further details are provided in the Appendix S1.

adder-counts were not different compared to the last 3y-adder-counts (Fig. S2). In moderate and severe impact sites, we found a very different pattern. Initial 3y-adder-counts were strongly negatively correlated with the last 3y-adder-counts ( $r = -0.989$ ,  $F_{1, 14} = 611.525$ ,  $P < 0.001$ ). The slope was steep  $-0.917$ , and during the last period of the study, many populations were extinct ( $N = 8$ ) while most others were reduced to less than 30% of their initial status ( $N = 6$  in strong decline). Even the initially largest population (S05) was almost extinct 5–6 years after the intensification of wild boar impact. Only two very small populations persisted in the moderate impact sites.

## Discussion

Wild boars play important roles as ecological engineers and as prey for large carnivores (Meriggi *et al.*, 1996; Sandom, Hughes & Macdonald, 2013; Hegel & Marini, 2018). Conversely during population outbreaks they become a pest (Barrios-García & Ballari, 2012). Our study reports such dramatic consequences on a snake species. In less than 10 years, wild boars provoked the strong decline or the extinction of most *Vipera berus* populations of southern Belgium.

Site occupancy analyses revealed that annual local extinction probabilities of adders on the severely and moderately impacted groups were 3.6 and 2.7 times higher, respectively, than in the low impact group (Fig. S1, Table 3). Wild boars also impacted the colonization probability of adders, which were 11.3 and 3.0 times higher,

respectively, in the low impact group than in the severe and moderate impact groups; colonization probability was extremely low in the severely impacted sites (Fig. S1, Table 3). As a result, site occupancy by adders in the severe impact group declined from 0.918 in 2005 to 0.473 in 2016, and from 0.825 to 0.687 in the moderate impact group while it remained high ( $>0.94$ ) in the low impact group (Fig. 3). In many cases, a single or few adders (i.e. known individuals characterized by their unique dorsal pattern) survived in strongly impacted populations, these regularly re-sighted adders generated a deceptive signal of population persistence. Adder-counts clearly revealed that beside a decrease in probability of occupancy, many populations actually collapsed or totally vanished in the severely impacted sites (Figs 4 and S2). Other populations where wild boar impact remained modest or undetectable over time were stable. But the continuous expansion of wild boars threatens them, and it may reach the few isolated populations of north Belgium.

Our results are straightforward: wild boars are rapidly becoming one of the main threats for snakes and likely for many other organisms; this situation needs an urgent response.

## Wild boar outbreaks

Demographic bulges are usually caused by a combination of intrinsic and external factors. The fast demographic strategy of wild boars predisposes them to population explosions (Kaminski *et al.*, 2005). Insufficient predatory pressure in Western Europe is due to the lack of large predators (Nores, Llana & Álvarez, 2008; Ripple *et al.*, 2014) and to declining numbers of recreational hunters (Massei *et al.*, 2015). Despite a progressive recovery of large carnivores populations accompanied by a timid re-appropriation of ancient distribution range, they are still totally absent from huge areas that cover most of Western Europe (Chapron *et al.*, 2014). Decrease of hunter numbers is aggravated by aging: in Germany 38% of hunters (men) were older than 65 years in 2016, and only 9% were in between 35 and 44 year old (Statista 2016). Reduced hunting pressure alone cannot explain the general augmentation of wild boar populations. Global changes, especially frequent mild winters and masting episodes, along with intensification of crop production (e.g. corn) bolster wild boars (Massei *et al.*, 2015; Frauendorf *et al.*, 2016; Gamelon *et al.*, 2017). Furthermore, in order to facilitate hunting, wild boars are familiarized through artificial feeding in winter while females and young are spared (hunters seek for large male-trophies); this practice minimizes famine risks and accelerates reproduction (Frauendorf *et al.*, 2016). Illegal breeding of wild boars with subsequent releases in the field also increase densities (examples on the Internet). More generally, hunters are not aware of their individual responsibility for wild boar population regulation (Keuling, Strauß & Siebert, 2016). Overall, global changes, lack of large predators, insufficient hunting pressure and questionable practices favor wild boar (Ickes, 2001; Massei *et al.*, 2015).

These multi-factorial causes explain that although the total numbers of hunters remain stable in Belgium, recreational hunting cannot keep ungulate populations in check (Licoppe *et al.*, 2014; Morelle *et al.*, 2016). In Wallonia, from 1985 to 2012, deer populations increased 3 times despite a proportional increase of kills. The situation for boars is worse with a 4.5 fold population increase despite a 2 to 8 fold increase of kills (Licoppe *et al.*, 2014). Wild boars found refuges in forests, notably bushy areas, and thus invade the patches used by reptiles and amphibians

### Snake population collapses

The most prosperous adder populations were initially situated in protected areas (Table 2). But protected sites offer major advantages to wild boars. Hunting is prohibited, boars are highly mobile and possess excellent spatial cognitive abilities; they rapidly learn to locate such refuges (Mendl, Held & Byrne, 2010; Prévot & Licoppe, 2013). Protected sites are usually fitted with rich habitats (e.g. ponds, thick bushes) and high species diversity. In addition, six severely impacted sites were initially managed to promote open and complex habitats (e.g. thanks to Life project funding), and to favor biodiversity, notably of reptiles and amphibians. Overall, important ecological requirements for reptiles and wild boars were overlapping in the 'best' sites. Highest wild boar densities have been precisely recorded in those areas that sheltered the largest adder populations twelve years ago (Fig. 1 and Fig. S3). In different monitored sites, artificial feeding further attracted wild boars (Table 1). Thus, for various reasons, wild boars intensively used the most favorable sites for adders and other reptiles. Consequently, initial prosperity level of adder populations was a negative predictor of their decline (Fig. S2). Reptiles and amphibians are often the vertebrates that are the most rapidly threatened by wild boars (Taylor & Hellgren, 1997). Both direct predation and habitat destruction can lead to the adder population extinction. Wild boars severely impact habitats and rapidly affect the microclimates and the network of shelters needed by reptiles (Brunet *et al.*, 2016; Lecq *et al.*, 2017). In Belgium, wild boar overabundance also impacts other snake species. Two previously abundant species (notably in most adder sites), the grass snake *Natrix helvetica* and the smooth snake *Coronella austriaca*, vanished or strongly decreased (pers. obs.). Jolley *et al.* (2010) estimated that 3000 wild boars consume more than 3 million reptiles and amphibians per year; even a small fraction of this estimate represents a major threat to snakes in Belgium.

Fluctuations of trophic resources can strongly impact, growth, fecundity and thus adder populations (Madsen & Stille, 1988; Bonnet *et al.*, 2001). However, this factor cannot explain the trends observed for several reasons. Prey and predator populations often exhibit coupled fluctuations, crashes are followed by recovery phases (Hanski, Hansson & Henttonen, 1991). Rodent population fluctuations tend to be spatially synchronized (Ranta *et al.*, 1995). We observed a very different pattern: two temporally contrasted types of trajectories (stable vs. collapsing predator populations).

Rarefaction of predators relaxes the pressure exerted on lower trophic level allowing for a rebound of prey and predators without extinction (Korpimäki & Norrdahl, 1998). Instead, following initial adder collapses we did not observe any sign of recovery and eight populations eventually became extinct. Furthermore, adders do not feed exclusively on rodents (e.g. voles); they eat various prey, shrews, amphibians or lizards that exhibit totally different ecology and life-history traits compared to small rodents. It would have been remarkable to observe a simultaneous rarefaction of all the prey types exclusively in the impacted sites. Indeed, the likelihood for all prey rarefaction as the primary cause for snake decline exclusively on those adder populations impacted by wild boars during 8 years in 14 sites, but not in the 9 other sites spared by wild boars, and all that independently from the impact of wild boars, is very low. The same reasoning applies for alternative factors (climatic factors, epizooties, inbreeding...). More likely, wild boars were the primary cause for adder collapses, directly (e.g. killing snakes) and/or indirectly via prey depletion and habitat destruction. Consequently, assessing rodent availability or including climatic variables in the analyses was not necessary to ascertain that local wild boar outbreaks were the main cause for snake collapses, especially because intensive rooting also entails rodent and habitat destruction (Fagiani *et al.*, 2014).

Our results support the hypothesis proposed more than 40 years ago: ungulates can provoke large-scale destruction of reptiles (Janzen, 1976). They demonstrate that several authors correctly assumed that wild boars may represent a threat to snakes, including adders (Filippi & Luiselli, 2002; Völkl & Thiesmeier, 2002; Lenders & Jansen, 2010). Yet, previous studies were preliminary and limited in their ability to show that wild boars actually pose conservation problems for snakes. For example, in the single scientific publication available (Filippi & Luiselli, 2002), only two plots were surveyed during a brief period and few observations were collected (10 vs. 36 snakes). Thus, no decline and no extinction could be documented, and no replicate was available: various alternative explanations for the difference of snake count between the two spots could not be discarded.

Our study reports large-scale effects on 23 populations monitored during more than 10 years, and it reports the first cases of extinctions. Consequently, this study demonstrates for the first time that wild boars can have devastating effects on snake populations.

### Conservation actions

Facing the demographic explosion of wild boar there is no simple response (Toïgo *et al.*, 2008). Wild boars target the most important sites for the conservation of adders and of associated species and ecosystems. To prevent the total extinction of snakes, selected sites should be fenced. The effectiveness of this measure has been demonstrated for reptiles (Lenders & Leerschool, 2014). High logistical costs mean that this measure can be applied to few small sites. Yet, wild boars can ruin long-term efforts to promote

biodiversity. In the current study they annihilated management actions to favor reptile and amphibian communities, and thus already wasted considerable resources (notably LIFE actions).

Limitation of wild boars proved to be successful to protect reptiles (Cruz *et al.*, 2005). However, demographic responses of wild boars can compensate for increasing hunting pressure (Servanty *et al.*, 2011). In order to limit outbreaks it has been recommended to target reproductive females and piglets; roughly, 80% of them should be killed annually (Toigo *et al.*, 2008; Keuling *et al.*, 2013).

To preserve highly fragmented sites favorable for reptiles that persist in North Western Europe, combined actions might be necessary: fencing the most fragile spots, reinforcement of regulation against illegal wild boar farming, prohibition of winter feeding, and encouragement to remove females and piglets are urgently needed before uncontrollable and irremediable damages occur.

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## Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

### Appendix S1. Supplementary material

**Table S1.** Definition of the parameters used in the multiyear robust design occupancy models with relaxed closure.

**Complementary captions to Figure 4.** Repeated measures ANOVA show a strong effect of wild boar on the numbers of adders observed over time

**Figure S1.** Estimation of extinction (top panel) and colonization (bottom panel) probabilities by adders (*Vipera berus*) in 23 sites monitored during 12 years in Belgium

**Figure S2.** Difference between mean adder-counts (*Y*-axis) during the first three years (2005–2007) and the last three years (2014–2016) of the study in function of initial 3y mean adder-count (2005–2007)

**Figure S3.** In this map, the density of wild-boars is expressed using two approaches based on the number of kills recorded in 2012