


Response of farmland reptiles to agricultural intensification: Collapse of the common adder *Vipera berus* and the western green lizard *Lacerta bilineata* in a hedgerow landscape

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Abstract

Agricultural landscapes cover a large portion of the planet and the intensification of farming is a primary cause of biodiversity loss. Changes in agricultural practices have been particularly marked in Western Europe over the last century. Hedgerow landscapes consist of complex mosaics of pastures, ponds, and hedges connected with forest patches that are favourable for biodiversity. Recently, however, these traditional farming landscapes have been profoundly simplified with a massive reduction in hedgerows. Reptiles are currently facing an important global decline, but the impact of the intensification of agricultural practices on their populations remains understudied. We studied the common European adder *Vipera berus* and the western green lizard *Lacerta bilineata* in Western France in a hedgerow landscape undergoing agricultural intensification. We first quantified the habitat changes (density of hedgerows and forest edges) from 1950 to 2015. Second, we documented changes in the distribution of *V. berus* and *L. bilineata* in the area between two surveys conducted 18 years apart (survey 1: 1994–1997 and survey 2: 2012–2015). The two species were more likely to be found at sites with dense hedgerows and forest edges at the first survey. We detected marked range contractions in the distributions of both species over 18 years (92% and 74%, respectively, for *V. berus* and *L. bilineata*). Population monitoring of the adder with capture-mark-recapture at two sites revealed marked declines related to the degradation of hedgerows and closure of the forest patches. Our results underline the importance of traditional agricultural landscapes for biodiversity conservation and the value of squamate reptiles as indicator species in such landscapes.

Introduction

A global and rapid biodiversity loss is underway and is closely linked to human activities (Newbold *et al.*, 2015). The dramatic changes in land use involve the conversion of natural landscapes into urban, industrial, or agricultural areas (Newbold *et al.*, 2015, 2016). Agricultural landscapes now cover a large portion of the planet and clarifying how farming practices influence biodiversity is a major conservation issue (Foley *et al.*, 2005; Newbold *et al.*, 2016). Traditional farmlands are usually comprised of mosaics of semi-natural and modified habitats (Holland *et al.*, 2017; Sartorello *et al.*, 2020). The intensification of agricultural practices, however, has resulted in major landscape structure simplification and

in habitat loss (Foley *et al.*, 2005; Kremen, Iles, & Bacon, 2012). Industrial farming is now recognized as one of the primary threats to biodiversity and ecosystems (Stoate *et al.*, 2001; Gámez-Virués *et al.*, 2015).

In western Europe, traditional farming practices have shaped structurally complex landscapes consisting of a network of hedgerows bordering small pastures and cultivated fields, and connected with small forest patches (Burel & Baudry, 1995). These hedgerow landscapes have been profoundly degraded during the XXth century following a shift from extensive land use to intensive crop farming (Robinson & Sutherland, 2002). Mean field size increased through removal of hedgerows (over 500 000 km in France which represents 57% of the initial length). Subsequently, crop

monoculture (corn, wheat, canola) and fodder beet for cattle feeding have largely replaced traditional pasture fields (Bourgeois & Demotes-Mainard, 2000). Changes in agricultural practices have led to a drastic reduction in the number of farms and ensuing development of enlarged farming units with heavy mechanical/chemical use over large areas (Bourgeois & Demotes-Mainard, 2000). Meanwhile, the abandonment of small and less productive parcels associated with rural exodus resulted in encroachment of forest in remnant semi-natural habitat patches (Cavaillhes & Normandin, 1993).

Compositional and configurational heterogeneity are critical for biodiversity conservation in farmlands (Fahrig *et al.*, 2011). Hedgerow landscapes are a tight imbrication of natural and anthropized habitats (Baudry & Jouin, 2003) favourable to diversity of both vertebrates and invertebrates (Tourneur & Marchandeu, 1996; Ouin & Burel, 2002; Michel *et al.*, 2007; Boughey *et al.*, 2011; Boissinot, Besnard, & Lourdais, 2019). Population density and species richness are much higher in dense hedgerow networks connecting diverse habitats than in purely agricultural landscapes (Boissinot, Besnard, & Lourdais, 2019). Microhabitat quality also affects biodiversity, notably hedgerow structure and the presence of herbaceous borders (Ouin & Burel, 2002; Graham *et al.*, 2018). The impact of hedgerow landscape degradation on biodiversity has been documented in several groups. For instance, hedgerow loss is detrimental to insects (Chamberlain *et al.*, 2000), birds (Cornulier *et al.*, 2011), amphibians (Arntzen *et al.*, 2017), and rodents (de la Peña *et al.*, 2003).

Reptiles are currently facing important declines worldwide (Gibbons *et al.*, 2000; Doherty *et al.*, 2020), but the impacts of intensive agriculture remain understudied (Ribeiro *et al.*, 2009; Biaggini & Corti, 2015). This lack of information is problematic because many reptiles, notably squamates (lizards and snakes), use agricultural lands as secondary habitats (Naulleau, 2002; Wisler, Hofer, & Arlettaz, 2008). Reptiles frequently occupy hedgerows, forest edges, and other anthropic habitats such as stone walls (Wisler, Hofer, & Arlettaz, 2008; Reading & Jofre, 2009; Lelièvre *et al.*, 2010; Martinez-Freiria, Lorenzo, & Lizana, 2019). Such linear habitats offer multiple benefits to reptiles, including microhabitats for thermo and hydoregulation, shelters, and food (Blouin-Demers & Weatherhead, 2001; Guillon *et al.*, 2014). These linear habitats also facilitate dispersion and thus connectivity between populations (Wisler, Hofer, & Arlettaz, 2008). While squamate reptiles are often encountered along hedgerows, only a few studies have considered reptiles in hedgerow landscapes (Hansen *et al.*, 2019). To the best of our knowledge, no previous study has addressed the impact of hedgerow loss on squamates. Because of the absence of population monitoring dating back to World War II, it is impossible to assess the impact of initial hedgerow loss on squamates in Western Europe. Population surveys over the past twenty years, however, can provide information on the impact of more recent hedgerow loss on squamates.

We studied a typical hedgerow landscape in Western France (Loire Atlantique). The study area (approximately 45 km²) has

been impacted by the intensification of agricultural practices typical of Western Europe (Almandoz, Colson, & Stenger, 1996; Guy & Maréchal, 2018). We studied the European adder *Vipera berus* and the western green lizard *Lacerta bilineata*, two excellent candidates to assess the impacts of intensive agriculture because both species occupy a diversity of natural habitats (heathlands, rocky outcrops) and are also frequently encountered in traditional farmlands (Saint Girons & Duguy, 1976; Guiller & Legentilhomme, 2006; Guiller, Legentilhomme, & Lourdais, 2014). Both species also have limited movement capabilities and are sensitive to perturbations (Sacchi *et al.*, 2011; Gardner *et al.*, 2019). In this context, we wanted to address the following questions:

1. How much has the agricultural landscape changed over the last 65 years in our study area? We quantified hedgerow density and forest cover in 1950 (initial state), 1993 (post-hedgerow loss), and 2015 (current intensive crop farming) based on aerial photographs to document landscape changes.
2. Have the landscape modifications changed the distribution of adders and green lizards in our study area over nearly 20 years? We documented the occurrence of both species in 715 cells in 1994–1997 and in 2012–2015.
3. Have the landscape modifications caused population declines of adders over nearly 20 years? We assessed population dynamics through capture-mark-recapture at two sites between 1999 and 2011.

Materials and methods

Study species

We studied the European adder *Vipera berus* and the western green lizard *Lacerta bilineata*, two squamate reptiles frequently encountered in traditional farming landscapes. Both species are frequently encountered along hedgerows, often using the herbaceous margins. Both species also use abandoned fields when the herbaceous and shrub cover (*Rubus*, *Ulex*, *Prunus*) offers a diversity of shelters and microhabitats (Guiller, Legentilhomme, & Lourdais, 2014). The European adder (Supporting Information Figure S1A) is a cold-adapted viviparous species with a large Euro-Siberian distribution (Sillero *et al.*, 2014). The adder is relatively small (mean SVL ≤ 55 cm), relies on sit-and-wait foraging, and typically occupies heathland, peat bogs, and traditional agricultural landscapes. Despite a large geographic distribution, adder movements and dispersal are limited, resulting in genetically structured populations (Madsen, Stille, & Shine, 1996; Ursenbacher *et al.*, 2009). The European adder is particularly vulnerable to anthropogenic perturbations including habitat degradation (Madsen, Stille, & Shine, 1996; Gardner *et al.*, 2019), wild boar predation (Graitson, Barbraud, & Bonnet, 2019), and climate change (Lourdais *et al.*, 2013). The western green lizard (Supporting Information Figure S1B) is a medium-sized oviparous species (mean SVL ≤ 12 cm) with a temperate and Mediterranean distribution (Sillero *et al.*,

2014). This conspicuous lizard occupies a diversity of habitats including rocky outcrops and dry heathlands. The western green lizard is thermophilic and often found on sun-exposed habitat edges (Sacchi *et al.*, 2011). In farmland, the western green lizard is often associated with hedgerows and roadsides (Saint Girons & Duguy, 1976). While limited data are available on population trends, there appears to be negative impacts of linear habitat degradation (Pérez-mellado *et al.*, 2009) and increased road traffic (Meek, 2009, 2020) on green lizard populations. The green lizard is also sensitive to habitat closure and can respond positively to cattle grazing (Pernat *et al.*, 2017).

Study area and landscape changes

Our study area (approximately 45 km², Figure 1) is located in Western France (Loire-Atlantique) in the commune of Bouvron (47°25'00"N; 1°50'49"W) and is composed of a mosaic of pastures and cultivated fields within a network of hedgerows (Supporting Information Figure S1C and D). Records from 1843 indicate that the area was composed of

478 ha of forest, 1380 ha of heathland, and dense hedgerows (Tremblay, 1993). Starting in 1963 and continuing today, the commune faced the nation-wide hedgerow removal and landscape conversion (Supporting Information Figure S1E and F). By 1978, the loss of heathland was 1277 ha (92%) and over 1000 km of hedgerows had been removed (Tremblay, 1993). Over time, mean field size has increased in response to the shift to industrial agriculture. The number of farmers has decreased in the area (Guy & Maréchal, 2018). The current landscape consists of crop fields (mainly corn, wheat, and colza) and cattle grazing with mechanized management of hedges (Supporting Information Figure S1G, H and I). Some less productive parcels have been abandoned and are rapidly reverting to thick shrubs and forest.

We quantified landscape variables within a grid of 715 [250 × 250 m] cells. Aerial photographs of the area were collected in 1950 (i.e. before massive hedgerow removal), 1993 (after hedgerow removal), and 2015 (current landscape). We quantified three variables reflecting hedgerow landscape composition: hedgerow density (m/ha), forest cover (m²), and density of forest edges (m/ha) by

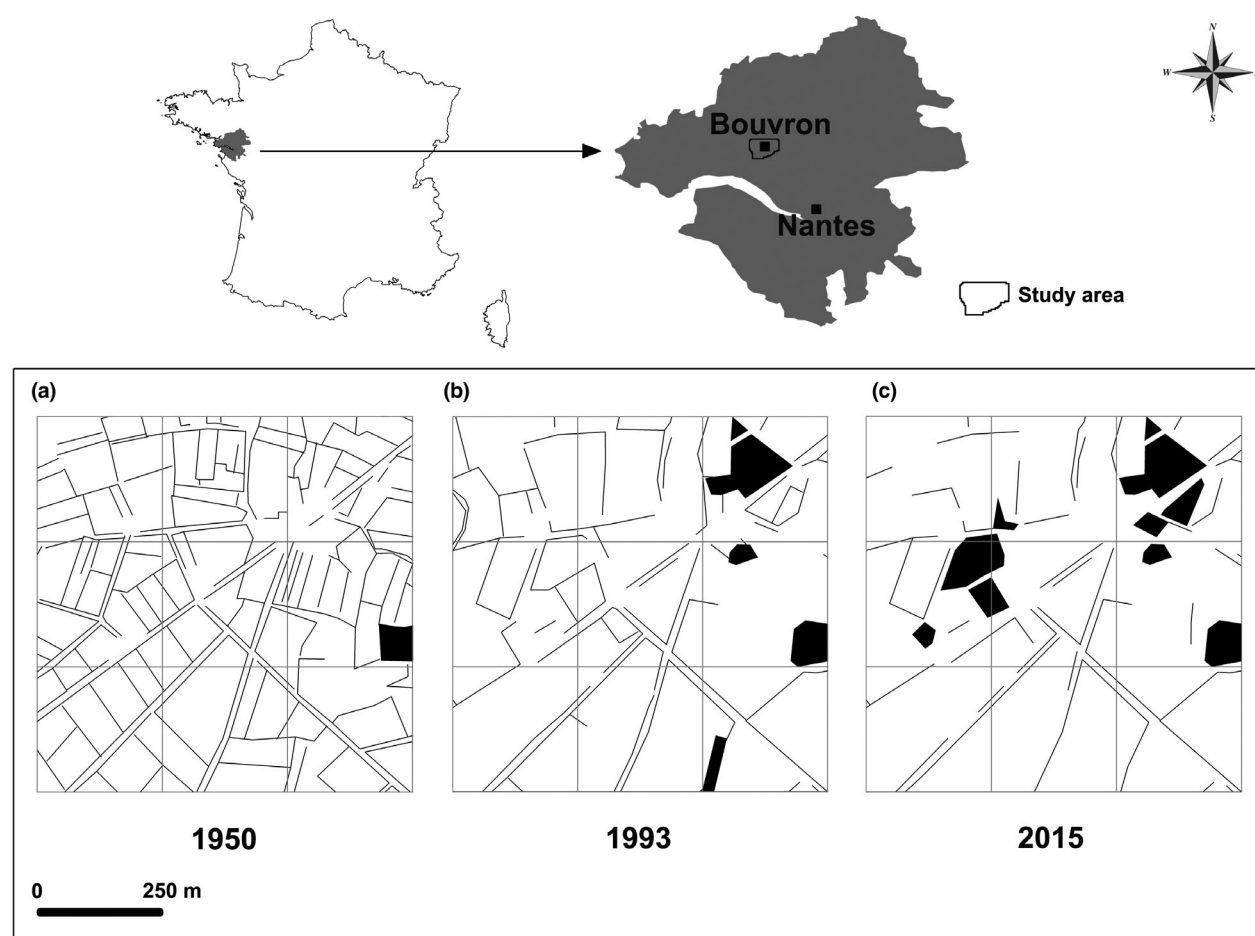


Figure 1 Location of the study site (commune of Bouvron) in Western France composed of 715 cells [250 × 250 m]. Landscape changes are illustrated for nine of the 715 cells in 1950 (a), 1993 (b) and 2015 (c). Hedgerows are represented by plain lines while black polygons indicate forest.

photographic interpretation of the geographic database BD Ortho® 2002 and BD Topo® 2002 (©IGN) in ARCGIS 9.2 (©ESRI). These landscape data allowed us to compare landscape composition at the three time points and to quantify the landscape changes between time periods (1950–2015, 1950–1993, and 1993–2015).

Species monitoring

Species detection

The two species are easily detectable in our study area, notably along habitat edges where individuals bask on sunny days (Guiller, Legentilhomme, & Lourdais, 2012, 2014). To provide an estimate of detection probability, we used visual observations collected at a site (La Gendronnais) near our study area and where the two species occur. The site was monitored from 1999 to 2018 (850 visits; see Supporting Information Tables S1 and S2) and also experienced habitat degradation. The mean per visit detection probability was 0.67 for *V. berus* and 0.55 for *L. bilineata* (Supporting Information Tables S1 and S2). Considering these probabilities, three visits allow to assess the presence with high confidence (cumulative detection probabilities $\geq 89\%$). Detection probabilities vary between months, however: detection probability was higher in spring (Supporting Information Table S2). Detection probability also varied between years and declined over time (Supporting Information Table S1) likely mirroring the decline in population size (Tanadini & Schmidt, 2011).

Species occurrence (*V. berus* and *L. bilineata*)

To determine species occurrence in the study area, we conducted two standardized visual encounter surveys 18 years apart in the 715 [250 × 250 m] cells that were used to document habitat changes. Each survey spanned 4 years (survey 1: 1994–1997 and survey 2: 2012–2015). During each survey, each cell was patrolled up to three times in different years. On sunny days in spring and early summer (February to June), we (GG and JL) walked slowly through suitable habitats (hedgerows, abandoned fields, forest edges, etc.) to detect vipers and lizards. We mapped the location of each individual detected with a GPS. We stopped visiting cells once the species had been detected in a given cell. While this approach can induce biases (Guillera-Arroita & Lahoz-Monfort, 2017), it was favoured to optimize the spatial coverage of the monitoring. The study was launched before the development of occupancy models and only the outcome of the successive visits (0 or 1) was kept on record. We accounted for imperfect detection by providing weights for cells with no detections (Gómez-Rodríguez *et al.*, 2012). We used observation data at the la Gendronnais site described above to estimate per visit probability of detection (P). To account for temporal changes in detection, we estimated, for each species, two P values as the mean detection probabilities over 4-year periods best approximating the timing of the two survey periods (Supporting Information Table S1). The estimated per visit detection probabilities were 0.78

(*V. berus*) and 0.64 (*L. bilineata*) for survey 1 and 0.59 (*V. berus*) and 0.52 (*L. bilineata*) for survey 2. This method allowed to consider changes in detection probability at the level of the study area, but it was not possible to account for spatial variation between cells. Following this approach, we examined the influence of landscape variables (hedgerow density, forest edges density) on species occurrence separately for each survey period. We also quantified changes in occurrence between the two surveys.

Population monitoring and demographic parameters (*V. berus*)

Adders were monitored by capture-mark-recapture at two sites: Haie was 6 ha and mainly composed of agricultural fields with hedgerows while Lande was 18 ha and mainly composed of abandoned fallow parcels. We visited each site at least 10 times each spring. Adders were captured, sexed, and individually marked by scale clipping (Guiller, Legentilhomme, & Lourdais, 2012). Haie was monitored from 1999 to 2007 and visited 189 times. In total, 57 *V. berus* were individually marked. Lande was monitored from 2002 to 2011 and visited 183 times. In total, 141 *V. berus* were individually marked. We ended population monitoring when we captured fewer than 2 individuals per year.

Capture histories of individual common adders were built by following the standard capture-mark-recapture (CMR) format for the Pollock's robust design (Pollock, 1982). The study consisted of nine primary (from the second half of February to the first half of November) periods covering 1999–2007 at the Haie study site, and 10 primary periods covering 2002–2011 at the Lande study site. Secondary samples consisted of two-week periods within each annual sampling season. Resighting data were pooled within each secondary sampling period. The adder populations were expected to be open to gains (immigration and recruitment) and losses (mortality and emigration) between years. Each primary period contained 18 secondary periods. The population was assumed to be closed to gains and losses among these secondary periods.

During our study, Haie was converted to corn production and this resulted in the structural degradation of hedgerows by mechanical management (hydraulic shrub grinder). Mechanical shrub grinding destroys the vegetation at the base of the hedge (Supporting Information Figure S1G and H) while the mature trees persist. Each year of monitoring, we measured the length of hedgerows managed with a shrub grinder and quantified the proportion of structurally degraded hedges. Lande witnessed habitat closure over our study because of parcel abandonment and ensuing forest regeneration. During each year of monitoring, we measured the proportion of trees and tall bushes (>2 m) as an index of habitat closure.

Statistical analyses

All statistical analyses were performed in R 3.5 (R Core Team, 2016) and R studio (version 1.3.9059) using the MASS, lme4, nlme, MuMIn, and AICcmodavg packages. Means are presented ± 1 SE unless otherwise stated.

Landscape changes

We used a log transformation on hedgerow and forest edges density to meet the normality assumption. We analysed changes in hedgerow density over time with a mixed model (lmer with a gaussian distribution) using year as a fixed factor and cell identity as a random variable. We examined total change in hedgerow density (final–initial) per cell with a linear model with initial hedge density as a linear covariate. We also compared changes in hedgerow density using a mixed model with time period (1950–1993 and 1993–2015) as a fixed factor, initial hedge density as a linear covariate, and cell identity as a random variable. We conducted a similar analysis with an estimate of annual loss of hedgerow density for each period (absolute loss divided by the time elapsed, i.e. 43 and 22 years). We analysed changes in forest cover in the 715 cells of our study area using a mixed model (glmer with a binomial distribution). Forest cover was the response variable (0/1), year was a fixed factor, and cell identity was a random variable.

Species occurrence

First, we examined changes in species occurrence between the two survey periods using a mixed model (glmer with binomial distribution) with species occurrence as the response variable and survey (1 or 2) as a fixed factor and cell identity as a random variable.

Non-detections in the three surveys were assumed to be absences; to account for imperfect detections, cells with no observations were weighted with the detection probability of the species in the corresponding survey period, following Gómez-Rodríguez *et al.* (2012). Detections were assumed to be completely reliable (weight = 1).

Second, we analysed the influence of landscape composition on species occurrence separately for each survey period (survey 1: 1994–1997 and survey 2: 2012–2015). For each period, we used generalized linear models (glm with binomial distribution) with species occurrence as the response variable and landscape variables as the predictors. Cells with no observations were also weighted with the detection probability of the species in the corresponding survey period. We compared five models including a constant model ($Y \sim 1$), three models with landscape variables for the corresponding survey ($Y \sim \text{Hedgerows}$, $Y \sim \text{Forest edges}$, $Y \sim \text{Hedgerows} + \text{Forest edges}$) and a model with habitat changes ($Y \sim \text{hedgerow loss}$) before the survey was conducted (hedgerow loss between 1993 and 1950 for survey 1 and between 2015 and 1993 for survey 2). We used stepwise model selection based on corrected Akaike's information criterion (AICc) to select the most appropriate model (delta AICc with the best model below a threshold of 2, Akaike weight > 0.9; Burnham & Anderson, 2002). We then used the best model to estimate parameters.

Demographic parameters

Kendall, Pollock & Brownie (1995) and Kendall, Nichols & Hines, (1997) developed full likelihood approaches that combine open and closed population models and that allow estimation of

a number of parameters from data collected under a robust design. We used a Huggins robust design Pradel model (Pradel, 1996) in program MARK (White & Burnham, 1999) to estimate demographic parameters and annual population sizes of adders at the two study sites while taking into account imperfect detection. Two kinds of sighting probabilities were modelled: P , the probability of seeing an individual in any secondary period for initial sightings and applied to individuals not previously seen in the primary period, and c , the probability of seeing an individual in any secondary period for resightings and applied to individuals previously seen in the primary period. Initially, we attempted to estimate sighting and resighting probabilities for each primary period (t), for each secondary period (i), and for each sex (sex), that is, $p_{sex}(t,i)$ and $c_{sex}(t,i)$, respectively. Due to sample size limitations, however, many parameters were not estimated. Sighting and resighting probabilities were thus constrained to be equal, were constant between secondary periods, but varied between primary periods and were sex dependent. The robust design Pradel model allowed estimating the following parameters during the primary intervals. Apparent survival probability (ϕ) is the probability for an individual to survive from primary period t to primary period $t + 1$. Recruitment rate (f) is the number of new individuals at primary period $t + 1$ per number of individuals at primary period t , and included immigration of new recruits from other locations as well as births between two closed capture sessions. Seniority probability (γ) is the probability that an individual was alive and in the population at primary session t was also alive and in the population at primary session $t-1$. Finite rate of population change (λ) is the population growth rate. Due to sample size limitations, parameters (ϕ , f , γ , λ) were constrained to be time constant, but varied between sexes. All parameters (ϕ , f , γ , λ) cannot be estimated simultaneously because they are effectively linear functions of each other. We thus chose different model structures that modelled ϕ , f , and λ because these were the parameters in which we were most interested. All these models were run independently for the Haie and Lande study sites. We used an information theoretic approach to select the most appropriate model for the data (Burnham & Anderson, 2002) based on the small-sample modification of the AIC (AICc, Hurvich & Tsai, 1989). Testing model fit in closed-population capture-recapture models remains an unresolved issue. We thus tested the fit of Cormack–Jolly–Seber open population models using program U-CARE (Choquet *et al.*, 2009) by pooling all secondary sessions of each primary session together and retaining only primary sessions. Finally, we used simple linear regressions to examine the relationships between annual population size estimates and landscape changes for each of the two sites monitored (hedgerow removal and habitat closure for Haie and Lande, respectively).

Results

Landscape changes

The hedgerow network was dense in 1950 (mean of 251 ± 3 m/ha) and hedgerows were found in almost all cells (710/715). There was a marked decrease in hedgerow density over time ($F_{(1,713)} = 908.99$, $P < 0.001$, Figures 1 and 2A):

the change from 1950 to 2015 was on average -155 ± 3 m/ha per cell which translates to a total loss of 722.6 km in the study area (62% of the initial network). Hedgerow loss from 1950 to 2015 was most severe in areas that initially had dense hedgerows (estimate = -0.72 ± 0.02 , $F_{(1,713)} = 908.99$, $P < 0.001$). When considering hedgerow loss over the two time periods separately (from 1950 to

1993 and from 1993 to 2015), we found that it was influenced by the period, initial density of hedges, and the interaction between the two (Table 1). Hedgerow loss was more pronounced in 1950–1993 (-131 ± 3 m/ha, total loss of 610.1 km, Table 1) than in 1993–2015 (-24 ± 1 m/ha, total loss of 112.5 km) and was most pronounced in cells that initially had dense hedgerows, but the relationship was stronger

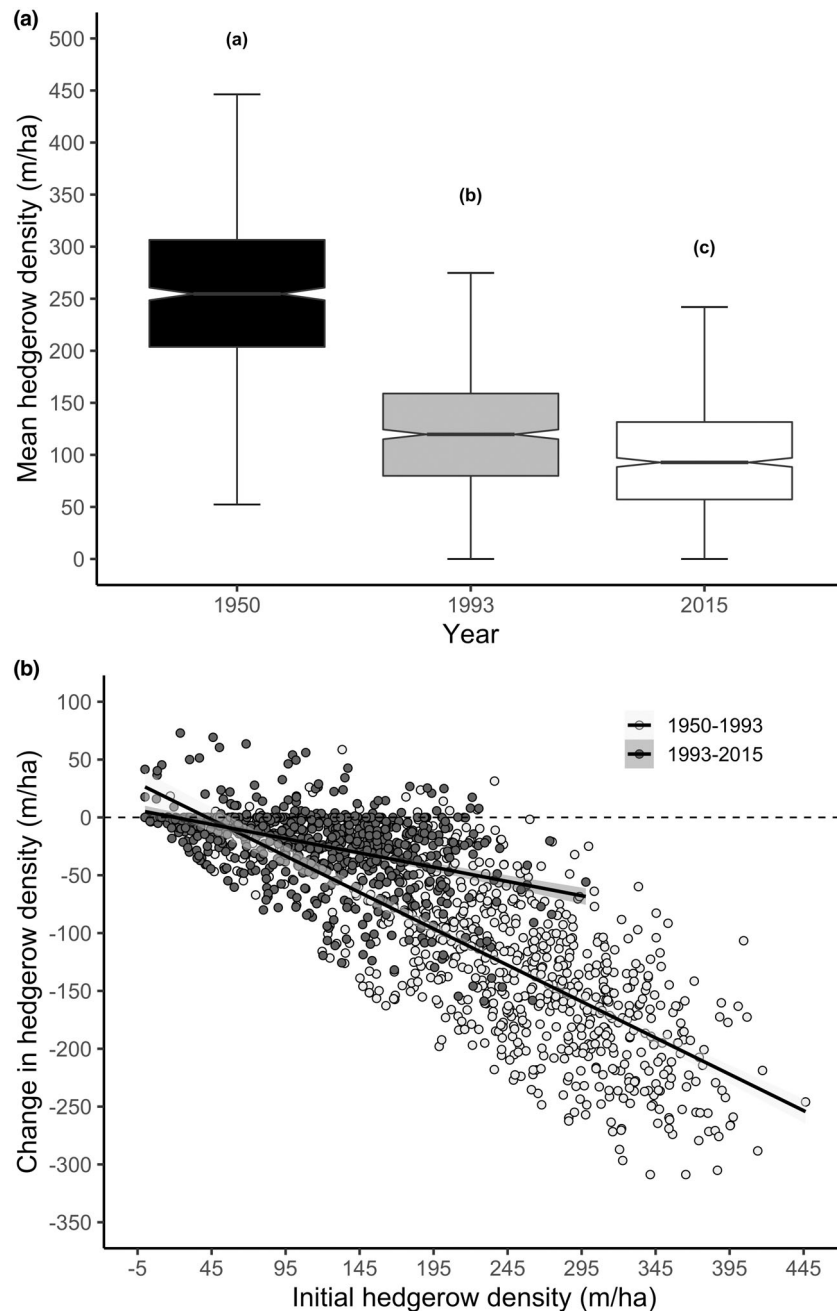


Figure 2 Changes in the hedgerow network in the study area in the commune of Bouvron in Western France. (a) Mean hedgerow density per cell (m/ha) in 1950, 1993 and 2015. (b) Change in hedgerow density (m/ha) per cell between 1950 and 1993 (grey circles) and between 1993 and 2015 (dark circles).

Table 1 Changes in hedgerow density per cell (m/ha) in the study area in the commune of Bouvron in Western France over two time periods (period 1: from 1950 to 1993 and period 2: from 1993 to 2015)

Response variable	LM type	Random effect	Explanatory variables	d.f.	F ratio	P value	Estimate	SE
Hedgerow changes (m/ha)	LMM	Cell identity	(Intercept)	714	1856.03	<0.0001	−76.99	4.73
			Initial Hedgerow length	712	2861.1	<0.0001	−0.82	0.01
			Period (1993–2015)	712	6778.56	<0.0001	10.59	4.35
			Interaction	712	19.62	<0.0001	−0.10	0.02

We tested the effect of period (fixed factor), initial hedgerow length at the onset of each period (linear covariate) and the interaction term. Cell identity was considered a random factor.

in 1950–1993 (Figure 2B). While hedgerow density strongly decreased in the study area, hedgerows were still found in almost all cells in 2015 (700/715).

Small forest patches were found in 276/715 cells at the start of the study (38%) and forest cover significantly increased over time ($F_{(2,712)} = 23.72$, $P < 0.001$) with forest patches found in 297/715 cells in 1993 (41.5%) and in 362/715 cells in 2015 (50.6%). Forest cover was significantly higher in 2015 than in 1993 and in 1950 (post hoc test, $P < 0.001$), but was the same between 1993 and 1950 (post hoc test, $P = 0.12$). The density of forest edges significantly increased over time from 39 ± 2 m/ha (1950) to 41 ± 2 m/ha (1993) and 46 ± 2 m/ha (2015). Post hoc tests revealed significant differences between years ($P < 0.001$), except between 1950 and 1993 ($P = 0.09$).

Changes in species occurrence

There was a massive collapse in the estimated occurrence of *V. berus* between surveys (initial: 0.26 ± 0.007 ; final: 0.03 ± 0.009 ; Type II Wald Chi square tests = 62.815 $P < 0.001$). During the first survey (1994–1997), we detected *V. berus* in 156/715 cells (Figure 3a) while during the second survey (2012–2015), the species was detected in only 13/715 cells (92% decrease, Figure 3c). Using model selection, we found that occurrence at the first survey was best explained by combining the additive effects of current hedgerow and forest edge density (Table 2, Figure 4a and b). At the second survey, species occurrence was best explained by hedgerow loss with a negative influence on species presence (estimate \pm SE = -0.59 ± 0.21 , Table 2), but the support (wi) for this model was 0.69. Another model suggested a positive influence of forest margin on occurrence (estimate \pm SE = 0.42 ± 0.21 , Table 2).

We also found a collapse in estimated occurrence between surveys in *L. bilineata* (initial: 0.09 ± 0.01 ; final: 0.01 ± 0.002 ; Type II Wald Chi square tests = 50.02, $P < 0.001$). The species was detected in 58/715 cells (Figure 3b) during the first survey, but in only 15/715 cells during the second survey (74% decrease, Figure 3d). Initial observations were best explained when combining the positive influences of current hedgerow and forest edge density (Table 2, Figure 4c and d). Species presence during the second survey appeared related to hedgerow loss, but this model had limited support (wi = 0.45) and was not different from the constant model ($\Delta AICc = 0.9$, see Table 2).

Demographic parameters and changes in abundance

At the two sites where we monitored vipers by capture-mark-recapture, the number of captures per year decreased significantly through time and eventually reached zero (Supporting Information Table S3). Goodness-of-fit tests of the Cormack–Jolly–Seber model did not indicate lack of fit (Lande: $\chi^2 = 19.04$, d.f. = 26, $P = 0.835$; Haie: $\chi^2 = 2.67$, d.f. = 9, $P = 0.976$). For both study sites, capture probability of adders varied between years, but not between sexes (Table 3). Capture probabilities decreased during the study periods at both sites (Figure 5b). Apparent survival and recruitment did not differ between sexes (Haie: 0.452 ± 0.044 (SE) and 0.189 ± 0.039 , respectively; Lande: 0.540 ± 0.036 and 0.340 ± 0.036 , respectively; Figure 5a). At Haie, the estimated total population size (males and females) declined from 51 (95% CI: 47–67) individuals in 1999 to 3 (95% CI: 2–22) individuals in 2007 (Figure 6a), with a population growth rate of 0.642 (95% CI: 0.555–0.720). At Lande, the estimated total population size (males and females) declined from 56 (95% CI: 49–76) individuals in 2002 to 24 (95% CI: 7–107) individuals in 2010 and finally 0 in 2011 (Figure 6b), with a population growth rate of 0.880 (95% CI: 0.796–0.932). Thus, adder populations declined at a mean rate of 35.8% per year at Haie and 12% per year at Lande. We found that annual population size estimates were negatively related to the degradation of hedgerows at Haie (estimate -0.42 ± 0.06 , $F_{(1,7)} = 48.87$, $P < 0.001$, Figure 7a) and to habitat closure at Lande (estimate -2.35 ± 0.43 , $F_{(1,8)} = 29.11$, $P < 0.001$, Figure 7b).

Discussion

The intensification of land use is a major driver of biodiversity loss (Newbold *et al.*, 2016). In this context, semi-natural habitats are of critical importance for biodiversity conservation and the procurement of ecosystem services (Holland *et al.*, 2017). Quantitative data on the status of most reptile populations in anthropized landscapes are lacking (Doherty *et al.*, 2020). Our study in Western France illustrates how the simplification of traditional farming landscapes with extensive hedgerows can negatively affect reptiles. While the European adder and the western green lizard were initially widespread and abundant in the study area and associated with hedgerows, we documented a drastic decline in both the extent of occurrence and in abundance reflecting the changes in the habitat.

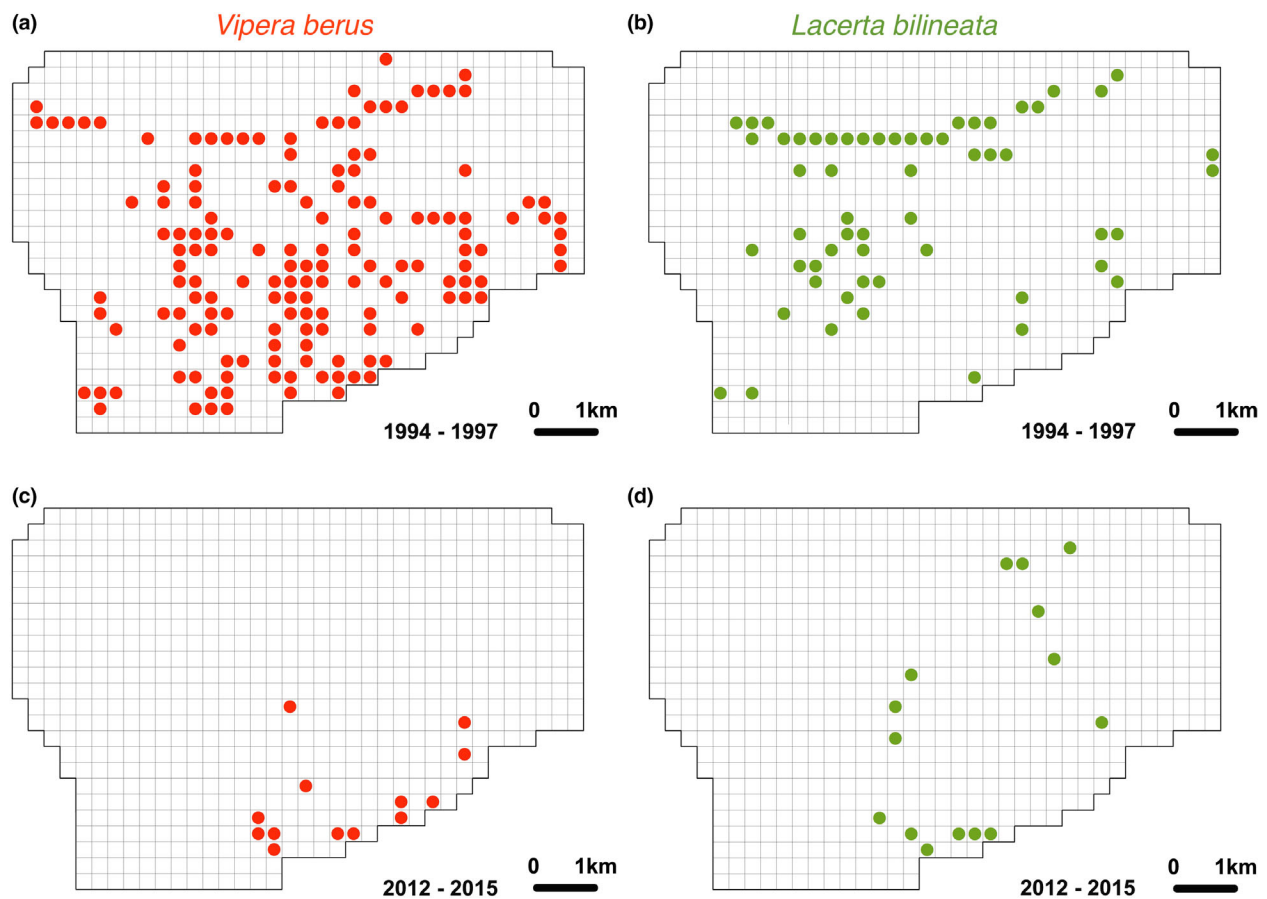


Figure 3 Observation of *Vipera berus* (a and c) and *Lacerta bilineata* (b and d) across the study area (715 cells, 250 × 250 m) in the commune of Bouvron in Western France during survey 1 (1994–1997) and survey 2 (2012–2015).

Landscape changes

Major changes in landscape structure have occurred over the past 70 years in Western Europe. These landscape changes reflect shifts in agricultural activity and land use since World War II in response to national and European policies (Bourgeois & Demotes-Mainard, 2000). While the number of active farmers in the Pays de la Loire Region was 187 554 in 1955, it decreased to 86 575 by 1988, and to 30 000 by 2016 (Guy & Maréchal, 2018). Over that period, hedgerow density decreased by 62% in the study area which is among the highest loss recorded (Boissinot, 2009). Most of the hedgerow loss was observed between 1950 and 1993 reflecting changes in agricultural practices and the increase in parcel size. Hedgerow removal continued between 1993 and 2015 owing to a reduction in the number of farms combined with a major increase in mean farm size (26.7 ha to 70 ha between 1988 and 2010; Guy & Maréchal, 2018). Farming shifted from traditional multi-crop to intensive crop farming with accompanying loss of cattle grazing and mechanized management of hedgerows. A clear trend in forest regeneration was also documented. Forest regeneration can be related to at least three phenomena: (1) abandonment of small

parcels has resulted in regeneration of small forest patches, (2) the progression of trees in non-agricultural patches (heathland, shrublands), and (3) plantation of poplars and/or evergreen for timber production. These combined changes have resulted in habitat simplification where we now have a landscape largely consisting of open fields bordered by degraded hedgerows and isolated forest patches.

Determinants of species occurrence

We observed a clear and massive collapse of two previously common squamate species in the study area with 92% and 74% decreases in observations for *V. berus* and *L. bilineata*, respectively. We were unable to account for spatial heterogeneity in detection, but we are confident that this possible source of bias could not explain the extremely strong diminutions. At the onset of monitoring (survey 1: 1994–1997), the European adder and the western green lizard occurred in most of the study area. Areas with dense hedgerows and forest edges were more likely to harbour vipers and lizards, indicating that the landscape was suitable even though declines had probably already started. However, the massive hedgerow loss that occurred previous to survey 1

Table 2 Determinants of the occurrence of *Vipera berus* (a) and *Lacerta bilineata* (b) in the commune of Bouvron in Western France for the two surveys (survey 1: 1994–1997 and survey 2: 2012–2015)

Period	Model	<i>k</i>	AICc	ΔAICc	wi	LogLike
(a) <i>Vipera berus</i>						
1994–1997	Hedgerow + Forest margins	3	733.43	0	0.93	−363.7
	Hedgerow	2	738.64	5.21	0.07	−367.31
	Forest margins	2	750.49	17.06	0	−373.24
	Hedgerow loss (1950–1993)	2	752.66	19.23	0	−374.32
	Null	1	760.06	26.63	0	−379.03
2012–2015	Hedgerow loss (1993–2015)	2	131.54	0	0.69	−63.76
	Forest margins	2	134.49	2.95	0.16	−65.24
	Null	1	136.19	4.65	0.07	−67.09
	Hedgerow + Forest margins	3	136.29	4.74	0.06	−65.13
	Hedgerow	2	138.2	6.66	0.02	−67.09
(b) <i>Lacerta bilineata</i>						
1994–1997	Hedgerow + Forest margins	3	386.49	0	1	−190.23
	Hedgerow	2	404.65	18.16	0	−200.32
	Forest margins	2	404.66	18.17	0	−200.32
	Hedgerow loss (1950–1993)	2	411.13	26.63	0	−203.55
	Null	1	416.58	30.09	0	−207.29
2012–2015	Hedgerow loss (1993–2015)	2	154.53	0	0.45	−75.26
	Null	1	155.43	0.9	0.29	−76.71
	Hedgerow	2	157.24	2.71	0.12	−76.61
	Forest margins	2	157.43	2.90	0.11	−76.71
	Hedgerow + Forest margins	3	159.26	4.73	0.04	−76.61

For each species and each survey period, we compared five models including a constant model ($Y \sim 1$), three models with landscape variables for the corresponding period ($Y \sim$ Hedgerows, $Y \sim$ Forest edges, $Y \sim$ Hedgerows + Forest edges) and one model with past habitat changes ($Y \sim$ hedgerow loss) before the survey was considered (between 1993 and 1950 for survey 1 and between 2015 and 1993 for survey 2). We used stepwise model selection based on corrected Akaike information criterion (AICc). The selected model appears in bold. *K* is the number of estimated parameters, ΔAICc is the difference in AICc between the current model and the lowest AICc model, wi is the AICc weight.

(between 1950 and 1993) was not retained in the best model, suggesting complex effects of habitat loss. During the second survey (2012–2015), the occurrence of vipers and lizards was spotty. An overall decrease in hedgerows density was observed between the two surveys and this variation influenced *V. berus* presence during the second survey, suggesting the strong role of the removal of hedgerows. In turn, the presence of *L. bilineata* during the second survey was unrelated to landscape variables possibly reflecting the ghost of past favourable habitats (Halstead, Wylie, & Casazza, 2014) or a reduced ability to detect habitat associations given the diminishing sample size. While the density of forest edges tended to increase over the study period, the hedgerow network density was diminished and what remained was profoundly degraded, thus affecting the ability of individuals to move between habitat patches (Davies & Pullin, 2007). The two species have limited dispersal abilities (Saint Girons *et al.*, 1989; François *et al.*, 2021) and habitat changes likely impede movements between sub-populations, which could negatively impact sub-populations even in favourable habitats. Overall, there was a clear and massive collapse of two previously common squamate species in the study area. Because of the dramatic reduction in connectivity (hedgerow loss) and the progression of forest cover (canopy closure), remaining populations are at risk in the short term

because of the possible extinction debt (Kuussaari *et al.*, 2009; Krauss *et al.*, 2010).

Population declines correlate with habitat degradation

Our capture-mark-recapture study of *V. berus* at two sites indicates the vulnerability of remnant populations to two sources of habitat degradation: structural degradation of hedgerows and habitat closure. While we detected a significant decline in both populations, it was more pronounced in the agricultural site of Haie (lower survival, lower recruitment probability, lower growth rate). Annual population size estimates at this site were directly related to the degradation of hedgerows by mechanical management (hydraulic shrub grinding) following the conversion of the site for corn culture. Mechanical management of hedgerows is closely associated with corn production and has devastating effects on the microhabitats available to reptiles (Supporting Information Figure S1G, H, and I). Mechanical hedgerow and forest edge management deteriorate habitat structure leading to abrupt transitions between field and trees which can increase exposure to predators (Hansen *et al.*, 2019) and affect biodiversity (Melin *et al.*, 2018). Such effects are insidious because hedgerows are still present, but their suitability for

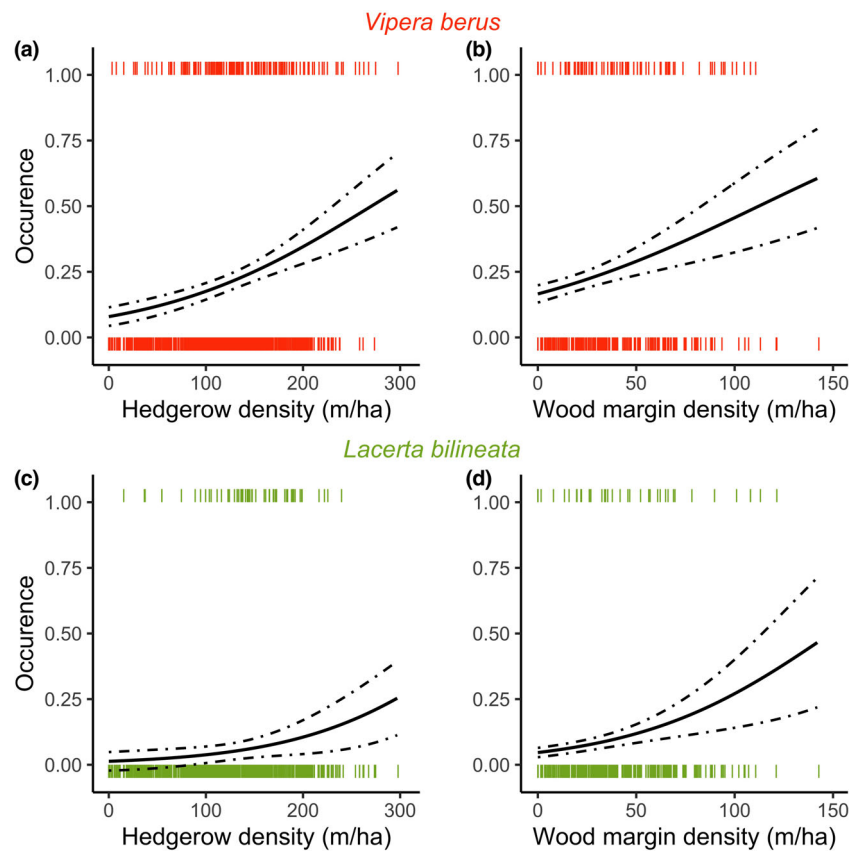


Figure 4 Influence of hedgerow density and forest edges density on *V. berus* (a, b) and *L. bilineata* (c, d) occurrence during the first survey in the study area (715 cells, 250 × 250 m) in the commune of Bouvron in Western France. Each vertical segment represents species occurrence (0/1). The plain line is the estimated slope and the dotted lines represent the 95% confidence interval of the estimated slope.

reptiles is strongly diminished by the removal of the herbaceous margin and associated refuges (Lecq *et al.*, 2017; Graham *et al.*, 2018). The abandoned fields of Lande were initially very suitable for reptiles with structured vegetation combining thick grass, small shrubs, and limited canopy cover. These microhabitats provide multiple benefits including basking sites, refuges, and food resources (Graitson, Ursenbacher, & Lourdais, 2020). The progression of trees and high bushes increased canopy cover and caused a gradual decrease in the number of observations. Canopy closure directly reduces habitat thermal quality and thus alters performance of ectotherms (Jofre, Warn, & Reading, 2016; Reading & Jofré, 2018). Thus, while abandoned fields can be temporarily favourable, vegetation succession and eventual canopy closure can lead to local extinction (Naulleau, 2002).

Agricultural intensification and reptile declines

The landscape changes we reported in our study area have also occurred on a regional scale in Western France (Bourgeois & Demotes-Mainard, 2000). The shift in farming practices has affected both linear habitats (field and forest edges)

and larger parcels with the loss of permanent pasture and grazed fields. We infer that the species declines we report over 18 years in our study area likely reflect a general decline in Western France and elsewhere where agricultural practices are intensifying. Reptile populations are facing important declines globally (Reading *et al.*, 2010; Doherty *et al.*, 2020). Because most lizards and snakes have limited movement capabilities, they are particularly vulnerable to microhabitat degradation. It is noteworthy that many squamates have found replacement habitats in anthropized environments (Graitson, Ursenbacher, & Lourdais, 2020). Traditional farming and hedgerow landscapes have a high structural and compositional heterogeneity due to the juxtaposition at a small spatial scale of grazed pastures, crop farming, and fallow fields. The continuing removal of hedgerows combined with the mechanical management of edges, however, have altered the quantity and quality of available microhabitats for reptiles and potentially other species. Additional factors related to agricultural intensification may also have contributed to the declines we observed in lizards and adders. Notably, the heavy use of pesticides associated with crop farming may have impacted the prey populations or resulted in direct effects on squamate populations (Gibbons, Morrissey, & Mineau, 2015). Finally, the increase in road

Table 3 Modelling the effects of year (t) and sex (s) on capture probability (p), recruitment probability (f) and survival probability (S) of adders at Lande and at Haie study sites

Model	Deviance	K	AICc	Δ AICc	wi
Lande					
S(.) f(.) p(t)	2472.1	11	3653.0	0.0	0.679
S(s) f(.) p(t)	2472.1	12	3655.1	2.1	0.236
S(s) f(s) p(t)	2472.0	13	3657.2	4.2	0.123
S(s) f(s) p(s,t)	2460.1	22	3664.9	11.9	0.002
S(s) f(s) p(.)	2519.7	5	3688.2	35.2	0.000
Haie					
S(.) f(.) p(t)	1594.3	9	2148.5	0.0	0.631
S(s) f(.) p(t)	1594.1	10	2150.5	2.0	0.237
S(s) f(s) p(t)	1593.7	11	2152.3	3.8	0.096
S(s) f(s) p(.)	1609.2	5	2155.1	6.5	0.024
S(s) f(s) p(s,t)	1582.5	18	2156.5	8.0	0.012

K is the number of estimated parameters, Δ AICc is the difference in AICc between the current model and the lowest AICc model, wi is the AICc weight.

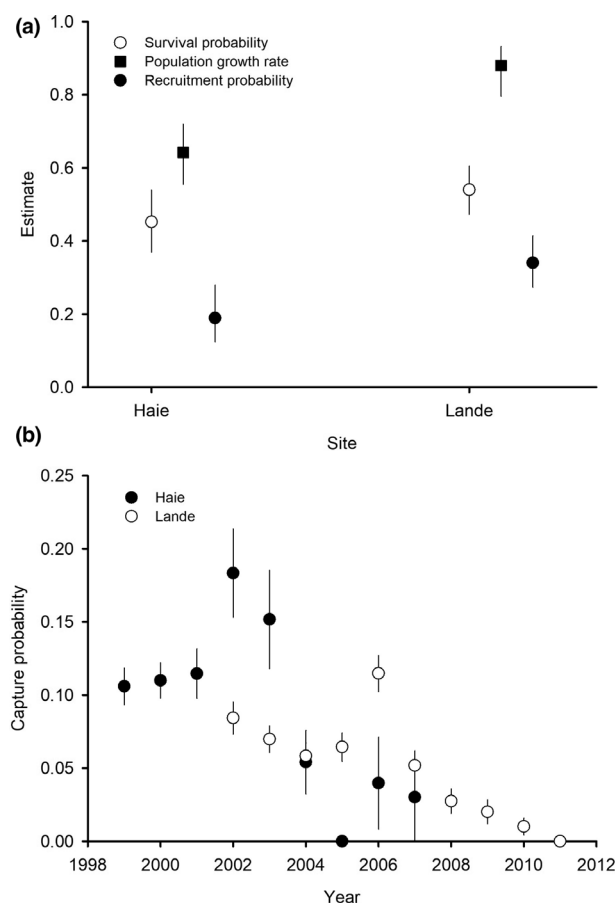


Figure 5 Estimates of capture probabilities over time for the two *Vipera berus* populations monitored in the commune of Bouvron in Western France (a). Estimates of survival probabilities, population growth rates and recruitment probabilities for the same two monitored populations (b).

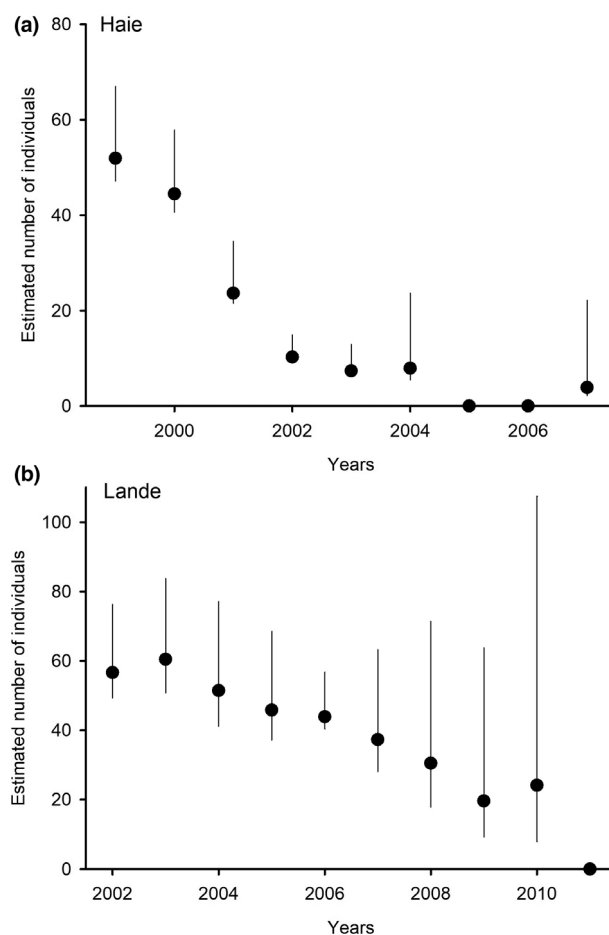


Figure 6 Annual population size estimates for *Vipera berus* in the commune of Bouvron in Western France at (a) Haie consisting of crop field hedges and (b) Lande consisting of abandoned fallow fields.

traffic and ensuing road mortality could be another contributing factor to population declines (Row, Blouin-Demers, & Weatherhead, 2007).

The global decline of previously common species was first identified as a pressing conservation problem by Gaston & Fuller (2007). We posit that the European adder and the western green lizard exemplify such declines following the degradation of linear habitats. The adder has several life-history traits (limited movement, low frequency of reproduction, high costs of reproduction) that make it vulnerable to perturbation. The species is also particularly sensitive to microclimatic conditions and vulnerable to water loss (Guillon *et al.*, 2014; Dezetter *et al.*, 2021). There are important declines of adders elsewhere, notably in small isolated populations (Gardner *et al.*, 2019; Graitson, Barbraud, & Bonnet, 2019). Our study extends these findings and indicates that declines are also occurring because of the negative impacts of intensive agriculture in areas where the distribution is relatively continuous. While the conservation status of the green lizard is less clear, this species also has specific

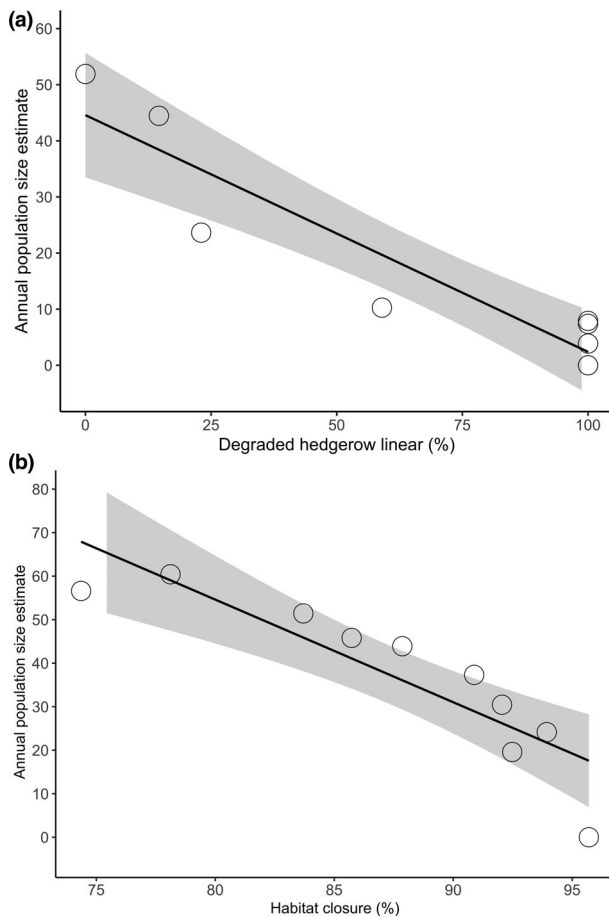


Figure 7 Relationship between annual population size estimates of *Vipera berus* and percent of hedgerows managed by shrub grinder for Haie. (a) Relationship between annual population size estimates and percent of habitat closure for Lande (b).

habitat requirements and limited mobility, and population declines have also been noted (Sacchi *et al.*, 2011). In cultivated lands, dense linear habitats with wide herbaceous margins are essential for biodiversity (Lecq *et al.*, 2017; Melin *et al.*, 2018). Permanent pastures and used land parcels provide essential habitat and shelters and can harbour large reptile populations (Graitson, Ursenbacher, & Lourdais, 2020).

Conclusion

Semi-natural linear habitats (hedgerows and forest edges) are essential for biodiversity and also provide important ecosystem services (Holland *et al.*, 2017). Reptiles have been neglected when considering the effects of farming practices on biodiversity. Our study suggests that squamate reptiles can be excellent indicators of the effects of agricultural intensification. The importance of hedgerows for biodiversity is now attracting increasing attention (Graham *et al.*, 2018) and notably the usefulness of structural restoration for farmland biodiversity (Staley *et al.*, 2015) or thermal buffering of climatic changes (Vanneste *et al.*, 2020). It is critical to

include reptile habitat requirements in hedgerow management practices. Other effects of the intensification of agriculture on reptiles deserve further study, such as the use of pesticides, the alteration of food resources, and reduced gene flow (Gauffre *et al.*, 2022).

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Ethics

This study was performed in accordance with laws relative to the capture and monitoring of *V. berus* and *L. bilineata* (DREAL permit #64/2016).

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Supporting information

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

Figure S1. (a) Female *Vipera berus* found basking at the base of a hedgerow. (b) Adult male *Lacerta bilineata* active in a hedgerow. (c) Suitable hedgerow bordering a pasture. (d) Suitable abandoned field with structured vegetation. (e) Complete removal of a hedgerow in the study site. (f) Remnants of a hedgerow removed from a field enlarged for corn production. (g) Mechanical cutting of large shrubs bordering a field. (h) Mechanical cutting of a hedgerow bordering a pasture. (i) Male *V. berus* found erratic and stressed after destruction of its habitat by a hydraulic shrub grinder.

Table S1. Variation in detection probabilities of *Vipera berus* and *Lacerta bilineata* between years at a site (“La Gendronnais”) located close to the study area and exposed to habitat degradation. We conducted 850 visits. The

detection probability per year was estimated from the ratio between the number of species detections and the total number of visits. The mean annual values are presented.

Table S2. Variation in detection probabilities of *Vipera berus* and *Lacerta bilineata* between months at a site (“La Gendronnais”) located close to the study area and exposed to habitat degradation. We conducted 850 visits. The detection probability per month was estimated from the ratio between the number of species detections and the

total number of visits. The mean monthly values are presented.

Table S3. Number of captures and recaptures for the two *Vipera berus* populations monitored on the sites of Haie and Lande. We used individual capture histories to build a robust Pradel model in program MARK (White & Burnham, 1999) to estimate demographic parameters and annual population sizes of adders at the two study sites while taking into account imperfect detection probabilities.