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Historical agricultural changes and the expansion of a water vole population in an Alpine valley

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ABSTRACT

Small mammal population outbreaks are one of the consequences of socio-economic and technological changes in agriculture. They can cause important economic damage and generally play a key role in food webs, as a major food resource for predators. The fossorial form of the water vole, *Arvicola terrestris*, was unknown in the Haute Romanche Valley (French Alps) before 1998. In 1998, the first colony was observed at the top of a valley and population spread was monitored during 12 years, until 2010. Spread occurred as a high population density wave. Based on farming history (1810–2003, 193 years) and spatio-temporal analysis of crop rotations, our study indicates that this water vole population outbreak has been promoted by the presence of grassland corridors that increase hayfield connectivity. These corridors appeared as a result of the conversion of cropped fields to hay meadows where water vole outbreaks have occurred. Spatial mosaic management for grasslands with decreasing spatial connectedness should be considered to prevent vole outbreak risks and promote biodiversity.

1. Introduction

Agricultural shifts generally correspond with technological and socio-economic changes (Allen, 2000). Mountainous regions are often considered to be favorable to biodiversity and more eco-friendly agricultural practices (Fjeldså et al., 1999). Currently, most areas in Europe have undergone either agricultural abandonment (and subsequent forest recolonization) or specialization (Chemini and Rizzoli, 2003). In developed countries, economic and technological changes in the 1950s led to specialized farming and geographically dissociated animal husbandry from cereal production. Thus, while vegetable and crop productions are now mostly located in the lowlands, farmers in mountainous regions have specialized in growing fodder for animal husbandry and milk production (García-Martínez et al., 2011; Cocca et al., 2012).

Today, in addition to agricultural intensification (increase of productivity in terms of quantity), specialization (production focused only on one or two crop types) is one of the greatest anthropic pressures on biodiversity and ecosystem services (Hole et al., 2005). Thus, while some species that depend on agro-ecosystems are declining (Fuller et al., 2005), others are considered to be pests because of the agricultural losses they cause (Singleton et al., 2010; Koyanagi et al., 2012; Krebs, 2013). The common vole (*Microtus arvalis*) and the water vole (*Arvicola terrestris*), are widely studied among other species, because both are potential pests to grassland (Krebs 2013).

There are many potential drivers of small mammal population outbreaks, and they are still under debate (Krebs, 2013). Small mammal populations are characterized by high intrinsic growth rates and strong inter-specific competition (Korpimäki et al., 2004). By increasing their food supply, agricultural intensification can promote the growth of small mammal populations (Morilhat et al., 2007). Additionally, agricultural specialization can modify landscape structure and composition, creating physical obstacles

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to small mammal dispersal or modifying the structure and composition of vole predator guilds (Delattre et al., 1992, 1996, 1999; Giraudoux et al., 1997; Duhamel et al., 2000; Morilhat et al., 2008; Falk et al., 2011). Outbreaks may also be driven by weather conditions (White, 2011).

In temperate Europe, early studies on the agricultural damage caused by voles focused on the common vole (*M. arvalis*). Spitz (1968), for example, reported extremely high damage (87% for Alfalfa and 100% for grass and wheat) in the lowland of Vendée, France after World War II. In mountainous areas, land-use policy led to specialize into grass production and to increase parcel size during the1960s–1970s (López-i-Gelats et al., 2011). Delattre et al. (1992) reported that multi-annual fluctuations of the common vole increased with the Ratio of Permanent Grassland to Farmland (RPGF). Similarly, in Franche-Comté, France, Giraudoux et al. (1997) found a 5–6 year cycle in *A. terrestris* population abundance beginning in the early 1970s on regional scale, after the expansion of permanent grassland. For grassland voles, episodic outbreaks become chronic when a scarcity or absence of forest is combined with grassland predominance across the landscape (Delattre et al., 1992; Giraudoux et al., 1997) or when the ratio of leguminous plants increases (Spitz, 1972; Delattre et al., 1992). Earlier works have documented that landscape changes may impact the kinetics of rodent populations (Hansson, 1979; Hansson and Henttonen, 1985; Eadie, 1953; Birney et al., 1976). Lidicker (2000) conceptualized these landscape effects with the Ratio of Optimal to Marginal Patch Area (ROMPA) hypothesis. In brief, variation in rodent abundance depends on the prevalence of their optimal habitat within a landscape. In addition, water vole outbreaks in Franche-Comté (also in the Massif Central) have been characterized by a spatial spreading over several years (Giraudoux et al., 1997; Berthier et al., 2013) called a traveling wave. Such pattern has also been documented for other species, such as the bank vole (*M. glareolus*) and the field vole (*Microtus agrestis*) in Finland (Hansson and Henttonen, 1985; Ranta and Kaitala, 1997) and the field vole (*M. agrestis*) in Scotland (Lambin et al., 1998; Bierman et al., 2006). However, long-term time-series and large scales data that would permit a detailed study of such processes are rare (Ryszkowski et al., 1971; Ryszkowski, 1982; Erlinge et al., 1982, 1983).

The presence of the water vole in the Northern Alps and its sporadic damage to grasslands and orchards are well established (Morel and Meylan, 1970; Meylan et al., 1971; Airoldi, 1976). The geographical complexity of valleys and the high altitude of mountains ranges were previously believed to prevent any large-scale spreading of small mammal outbreaks. The spatio-temporal patterns of water vole outbreaks have therefore not yet been documented in this context. In the Haute-Romanche valley, neither written records (e.g. direct or indirect, from predator diet analysis) nor oral tradition evidenced population outbreaks or even the presence of the water vole before 1998, when the first water vole outbreak suddenly occurred. Due to its proximity to the Ecrins National Park (*Parc National des Ecrins*, PNE) and the risks of exposing native wildlife to pest chemical control, this outbreak has been carefully monitored and mapped by the PNE staff. A few studies provided very local data describing the presence of the water vole in the Northern Alps, but did not mention potential outbreaks in those areas (Morel and Meylan, 1970; Meylan et al., 1971; Airoldi, 1976; Habert, 1988; Lapini and Paolucci, 1992; Saucy, 1994). Thus, the initial colonization of a valley where the species was previously absent has never been studied. The Haute-Romanche valley has undergone major land use changes since the 19th century (Girel et al., 2010; López-i-Gelats et al., 2011). At that time, mixed farming, including cattle husbandry, cereal and potato production was general. The valley began to specialize in animal (cow and sheep) breeding in the 1960s (Girel et al., 2010). In the 19th century, to promote crop production (potatoes, barley,

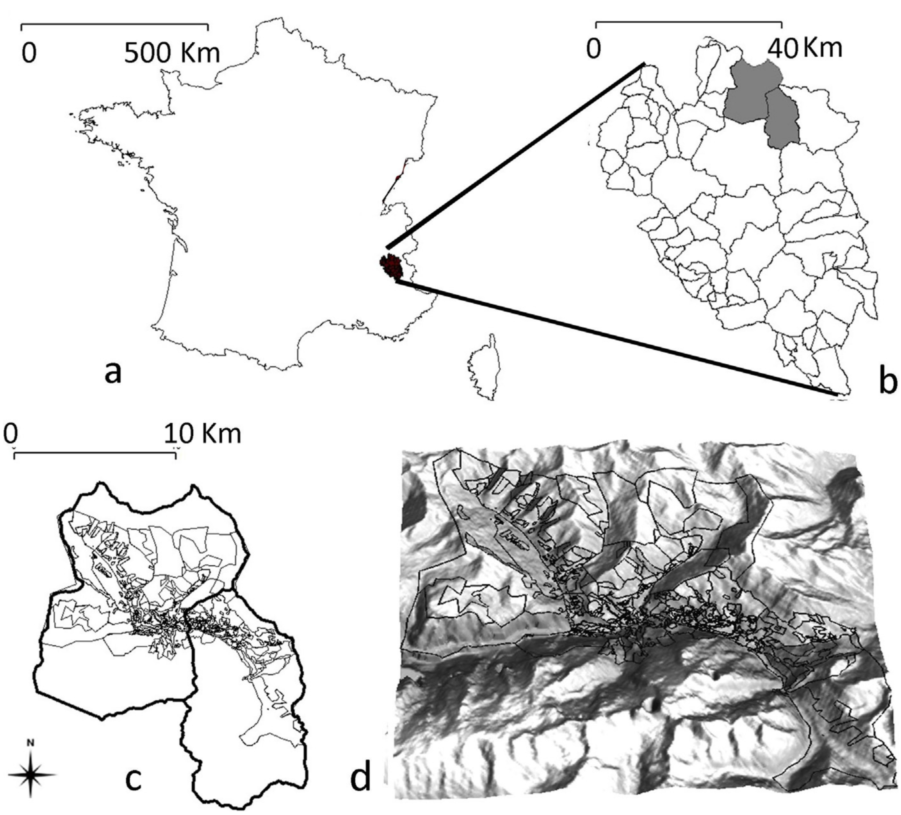

Fig. 1. (a) *Parc National des Ecrins* (PNE) (in black), (b) La Grave and Villar d'Arène communes (in grey) among the communes of the PNE(c) cadastral parcels in La Grave and Villar d'Arène (d) topography of the area (after Abrams et al., 2010).

wheat, etc.) and animal husbandry (grazing and mowing) in such challenging conditions, farmers modified the landscape by clearing forests and building field terraces at up to 2000 meters of altitude (Girel et al., 2010). These were abandoned during the 1960s–1970s with subsequent recolonization by grassland.

The aim of this study is to answer the three following questions: How has farmland in the Haute-Romanche valley evolved from 1810 to today? What were the spatio-temporal patterns of the water vole population in the Haute-Romanche valley during the 1998–2003 population outbreaks? Was colonization linked to current agricultural practices and/or with individual parcel farming history?

2. Material and methods

2.1. Study site

The study site was in the Haute-Romanche valley (45°02′49″N, 6°18′24″E), located in the sub-alpine and the lower alpine vegetation belts of the Alps (Fig. 1). Study site elevation ranged between 1300 meters at the *Fréaux* to 3976 meters at the *Meije* peak. Vegetation is subjected to cold temperatures (mean annual temperature 3.3 °C (Bocquet, 2001), and the growing season is very short (four months) and therefore unfavorable to intensive agriculture. The study area included two municipalities (*Villar d'Arène* and *La Grave*), which are part of the *Parc Naturel National des Ecrins* (Fig. 1). The valley primarily contains pastures (62%), meadows (4%), tillage (<1%) and larch forest (33%), and there are two main villages and scattered housing (Quétier et al., 2007; Lavorel et al., 2011). Farming mostly consists in breeding *Abondance* cattle for milk production in the neighboring *Savoie* region and breeding sheep for meat production. In summer, high-altitude pastures are grazed by local flocks in addition to a large number of transhumant sheep.

2.2. Data collection

2.2.1. Simplified land-use trajectories (SLUT) between 1810 and 2003

Land-use trajectories (LUT) were determined for each individual property (i.e., cadastral parcel) within the *Villar d'Arène* and *La Grave* municipalities. These trajectories were derived from the synthesis of three data sources: interpretation of aerial photographs from 1952, 1960, 1971, 1986, 1994 and 2001, historic data from land-use registers from 1810 and 1970, and recent data from interviews of local farmers in 1996 and 2003 (*Association Foncière Pastorale de Villar d'Arène*, unpublished data) (Quétier et al., 2007; Girel et al., 2010; Lavorel et al., 2011).

Lavorel et al. (2011) combined these data in a geographic information system (GIS) and documented past and present land use for the farmed areas within the municipality, using nine LUTs. Based on Lavorel et al. (2011), we simplified the land-use trajectories of the 721 cadastral parcels within the study area into simplified land-use trajectories (SLUT) (Table 1).

The percentage of each type of land use inside and outside the area where water voles were present during the time of the monitoring (1998–2010) was computed in the past and in 2003.

2.2.2. Water vole monitoring

The staff of the *Parc Naturel National des Ecrins* monitored and mapped the abundance of water voles in the Haute-Romanche Valley each year from 1998 to 2010 after the melting of the snow. The entire region was traveled to determine the spatial distribution and relative abundance of surface indices (earth tumuli, runways, etc.) via direct observation. Indices were scored using the following scale, adapted from Giraudoux et al. (1995):

- 0: no activity on the surface.
- 1: isolated indices.
- 2: <50% of the area colonized.
- 3: >50% of the area colonized.

The method used did not mean to represent the true abundance, but the activity of the water vole population. Giraudoux et al. (1995) have shown that this kind of index can be used as a proxy of relative abundance. Continuous areas with the same score were mapped as a polygon and stored in GIS as ESRI shapefiles. Polygons were then rasterized at a 5 m resolution for map algebra.

2.3. Temporal dynamics of the abundance of water voles at the cadastral-parcel scale

We computed the mean abundance score of each cadastral parcel in each year. For each cadastral parcel, we determined the first year with a mean abundance score above 0, which was considered to be the last year before the vole population outbreak. Water vole abundance dynamics from the first date of colonization of a parcel could thus be represented by this categorization, regardless of the geographical position of the parcel. Moreover, on the cadastral parcel scale, we studied the relationships between the intensity of the outbreak, the current land use (i.e., in 2003) and the SLUT.

2.4. Spatial spread of water vole population

We calculated the yearly speed of the population spread by measuring the minimal Euclidian distance between the most geographically advanced frontline at year "n" and the most advanced frontline at year "$n+1$".

2.5. Statistical analysis

We studied the annual variation of water vole abundance since parcel colonization, with abundance index as the response variable and year as an independent variable. We took possible non-linearities into account using a general additive mixed-effect

Table 1
Past land-use, land-use in 2003, land-use trajectories (LUT) and simpified land-use trajectories (SLUT).

Past land-use	Land-use in 2003	LUT	SLUT
Plowed once in the past	Plowed	LUT1	Plowed once in the past and plowed 2003
Plowed once in the past	Mown	LUT2	Plowed once in the past and mown in 2003
Plowed once in the past	Grazed	LUT3	Plowed once in the past and grazed in 2003
Mown once in the past	Mown	LUT4	Mown once in the past and mown in 2003
Mown once in the past	Grazed	LUT5	Mown once in the past and grazed in 2003
Mown once in the past	Unexploited	LUT6	Mown once in the past and unexploited in 2003
Grazed once in the past	Grazed	LUT7	Grazed once in the past and grazed in 2003
Unexploited	Unexploited	LUT8	Unexploited in the past and unexploited in 2003
Grazed once in the past	Grazed	LUT9	Grazed once in the past and grazed in 2003

model (GAMM) (Wood, 2006). Using GAMM allowed us to break the total variation into (i) the variation due to the fixed effect (here, the relationship between the response variable and the independent variable, $f_i(x_i)$) (ii) variation due to a random effect (here, the repetition of water vole abundance estimates on the parcel over time, $Z_i b_i$) and (iii) the residual variation of the model, Δ_i. Overall, the model relies on a link function, g (here, Gaussian), linking the response variable to the independent variable by the relationship:

$$g(E(Y)) = \mathrm{Xi}\theta + f_1(x_1) + f_2(x_2) + \ldots f_m(x_m) + z_i b_i + \Delta_i$$

Xi_θ is a row of the model matrix for any strictly parametric model component (Wood, 2006), and $f_i(x_i)$ is a nonparametric smoothing function (e.g., the sum of continuous sections of cubic polynomial splines calculated so that they are joined at points called nodes or knots) or a parametric function (without smoothing).

(1) The effects of current land use and SLUT were examined using a linear mixed model with the abundance index of water voles as the response variable, the current land use and SLUT categories as fixed effects, and parcel as a random effect to account for repeated measurements of each parcel. The relationship was the following:

$$y_i = x_i\beta + z_i b_i + \Delta_i$$

For statistical inferences, we used a permutation test ($n = 1000$) to avoid overestimating the degrees of freedom if spatial autocorrelation was present.

(2) The relationship of the minimal distance covered by water voles (y_i) and year (x_i) was calculated using a simple linear model.

We checked the validity of our model by comparing its AIC scores with that of a null model (Burnham and Anderson, 2002). To compare the values obtained for each category within our independent variables, we compared the AIC scores that we obtained to the null model.

2.6. Computing environment

Spatial analysis and GIS data management were conducted in Quantum GIS 1.8.0-Lisboa (Quantum GIS, 2013), GRASS GIS 6.4.2 (GRASS Development Team, 2012) and R 2.15.1 (R Core Team, 2012b) using the packages car (Fow and Weisberg, 2011), foreign (R Core Team, 2012a), maptools (Lewin-Koh et al., 2012), mgcv (Wood, 2011), pgirmess (Giraudoux, 2012), raster (Hijmans and van Etten, 2012), rgdal (Keitt et al., 2012), rgeos (Bivand and Rundel, 2012), Rlab (Boos and Nychka, 2012), and sp (Bivand et al., 2008).

3. Results

3.1. Past and present land use

In the past, grazed parcels were located at the highest altitudes, while mown and/or plowed parcels were located at the lowest altitudes within the Haute-Romanche Valley. Plowed parcels were generally in close proximity to settlements. By 2003, grazed areas had extended toward the valley bottom and settlements. Plowed areas had virtually disappeared, and mown areas decreased considerably.

Within the range of the water vole (from 1998 to 2010), the amount of mown area did not dramatically change (34.4% of the farmland area in the past compared with 34.6% in 2003, Fig. 2). However, outside of the water vole's range, the amount of mown area decreased from 8.8% in the past to 0.9% in 2003. Plowed areas declined both inside and outside the water vole's range, from 40.5% to 0.5% and 1.7% to 0.02%, respectively. Conversely, grazed areas increased both inside and outside the water vole's range, from 18.4% to 58.2% and from 53.4% to 63%, respectively.

3.2. Temporal dynamics of water vole abundance

Fig. 3 displays the inter-annual variations of *A. terrestris* abundance, according to the 2003 land-use categories. There was generally a dramatic increase in abundance during the year of colonization, peaking that year or the following, and then a slow

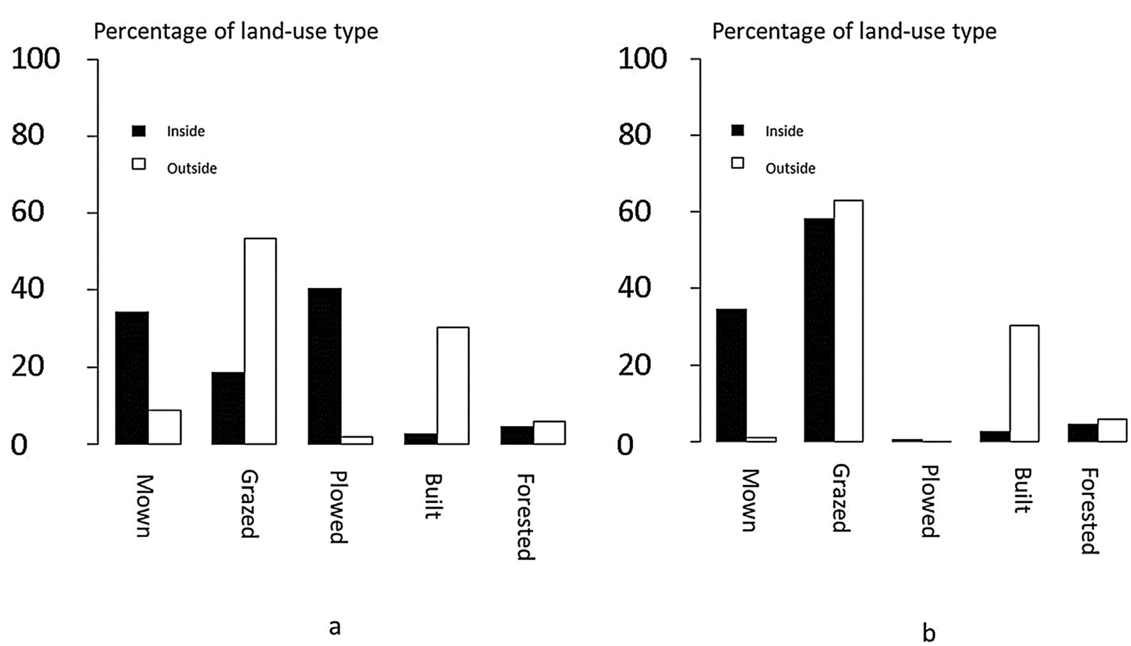

Fig. 2. Percentage of each type of land-use inside (black) and outside (white) of the area of presence of the water vole (1998–2010) in the past (a) and in 2003 (b).

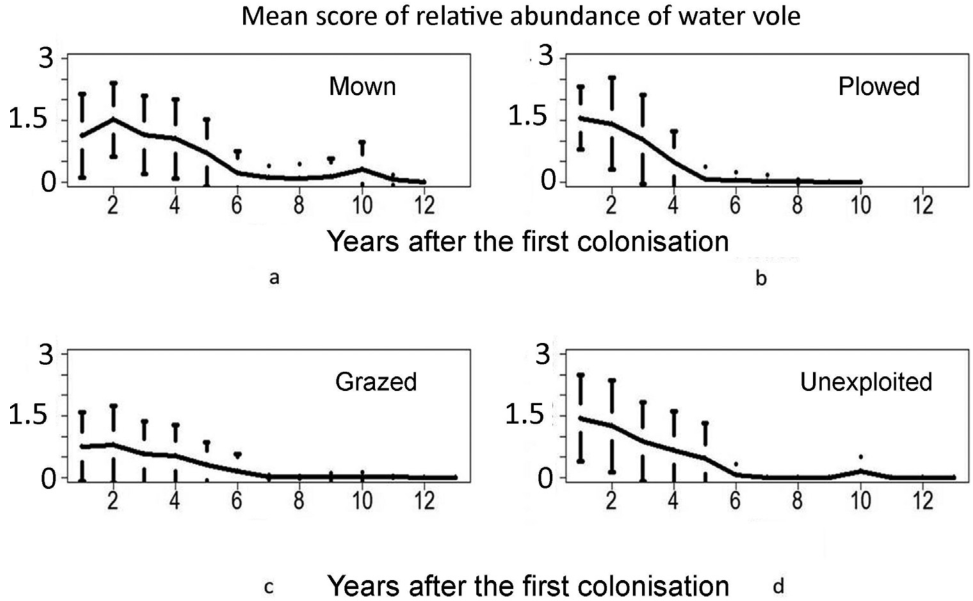

Fig. 3. Time variation of the mean score of water vole abundance for each parcel, from first colonization, according to land-use in 2003 (a: mown, b: plowed, c: grazed, d: unexploited).

decrease to low densities over the following 5 years (P-value < 0.0001).

The average abundance of *A. terrestris* significantly differed among the 2003 land-use categories ($R^2 = 0.02$; ΔAIC = 33, PermTest P-value < 0.0001) and was significantly lower in grazed than in mown parcels (ΔAIC = 27, Coef = −0.03).

The abundance of water voles also differed among SLUT categories ($R^2 = 0.03$; ΔAIC = 49). Parcels grazed in the past and continuing to be grazed in 2003 had a significantly lower abundance of water voles than the other parcels (ΔAIC = 45, Coef = −0.38).

3.3. Spatial spread of the water vole population

The first vole colonies were observed in 1998, near the *Chalet de la Buffe*. Other colonies were detected three years later, near the

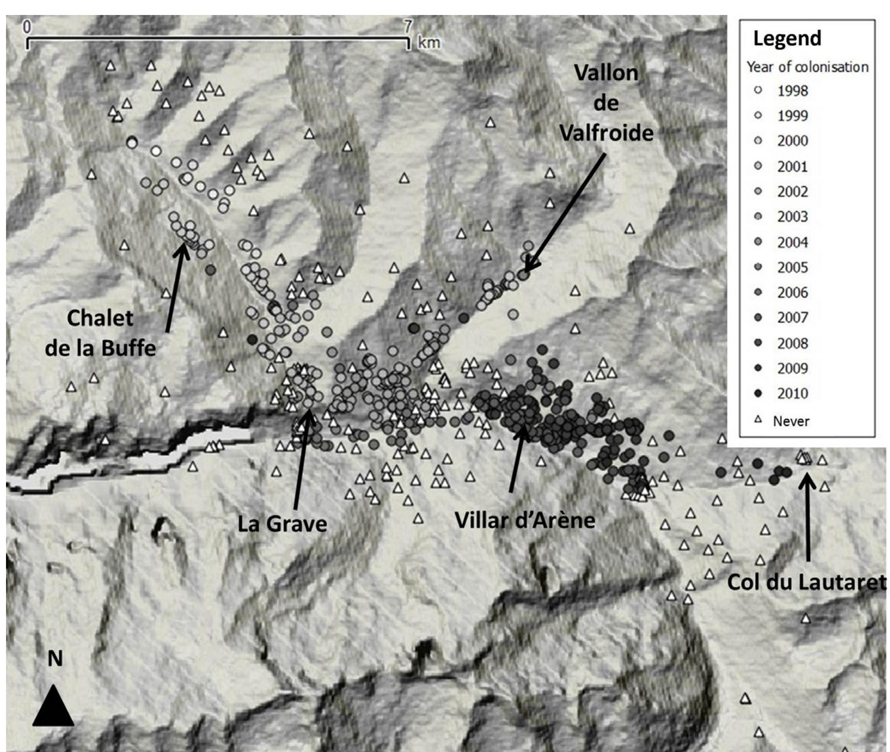

Fig. 4. Colonization by the water vole between 1998 and 2010.

Hameau de Valfroide. The vole colonization front moved from these two epicenters toward *La Grave* village within 5 years. The bottom of the Haute-Romanche Valley was reached in 2003, and the colonization front moved toward the *Col du Lautaret* through the *Villar d'Arène* village (Fig. 4). The general direction of colonization was northwest to southeast, following the Haute-Romanche Valley. However, the direction of spreading changed three times: southeast to northwest between 1998 and 1999, southeast to northwest between 2003 and 2004 and southeast to northwest between 2005 and 2006.

The distance covered each year by the water vole population significantly differed between years (ΔAIC = 197; R^2 = 0.22) (minimum = 500 m per year, median = 1500 m per year, maximum = 3700 meters per year).

4. Discussion

4.1. Past and present land use

In the past, areas that were distant from villages and farms were generally inaccessible to livestock, due to elevation and slope. Therefore, temporary settlements were established in summer pastures, and cattle and sheep were relocated to the valley during the winter months. Areas that were mown or plowed were close to farms in the valley bottom. The spatial organization of the Haute-Romanche valley reflects traditional land use patterns in mountainous regions worldwide (Nyssen et al., 2009; Girel et al., 2010; Pôças et al., 2011; Negi et al., 2012). Between 1810 and 2003, the landscape of the Haute-Romanche valley changed, following patterns consistent with most other Alpine valleys. Farming specialization in livestock breeding extended former grazing areas and led to a large decrease in mown areas for technical and economic reasons (subsidies sometimes made it more viable to purchase hay for cattle feed than to produce it locally on steep slopes) (Leynaud and Georges, 1965; Girel et al., 2010). An increase in farmer incomes during the second half of the 20th century and the concomitant expansion of the market to supra-regional scales led to the abandonment of subsistence and cash crop farming, thus leading to a dramatic decrease in plowed areas (Girel et al., 2010). Agricultural specialization is common in most mountainous regions worldwide to varying degrees (Huijun et al., 2002; Chemini and Rizzoli, 2003; García-Martínez et al., 2011). For example, in the Jura Mountains, grassland surface area represented approximately 40% of the total farmland in 1956 but approximately 100% in 1988 (Giraudoux et al., 1997). Similarly, Tasser et al. (2009) report that until the 1960s, the montane belt in South Tyrol (Italy) was composed of a mosaic of arable fields and grasslands, and shifted to 100% grasslands in the subsequent years. In Switzerland, over the same period, Maurer et al. (2006) showed that low-intensity grasslands farther from settlements were abandoned, whereas easily accessible grasslands were used more intensively (Kahmen et al., 2002) and were mown and fertilized more frequently (Bätzing, 2003).

In the Haute-Romanche valley, the amount of mown area within the water vole range did not change between 1810 and 2003. This finding may be important because high grass in mown areas for several months prior cutting is more favorable to the water vole than low grass of pastures and plowed fields (Morilhat et al., 2007).

4.2. Temporal dynamics of water vole abundance at the cadastral-parcel scale

The water vole population outbreak from 1998 to 2010 in the Haute-Romanche valley is similar in terms of temporal patterns to other areas where cyclic outbreaks occur (e.g., the Jura and the Massif Central Mountains). Considering the temporal aspect of the outbreak locally, we demonstrated a quick population increase (one year) in abundance followed by a non-linear slow decrease over the subsequent years In western Europe, water vole populations are usually cyclic, with a period of 5–7 years (Saucy, 1994; Giraudoux et al., 1997; Berthier et al., 2013). Here, we monitored the water vole population of the Haute-Romanche valley over thirteen years. At the parcel scale, we recorded only one outbreak during the first six years of observation. Moreover, we observed peak abundance during the very first year of colonization. One possible hypothesis is that the method we used (i.e., scoring very large areas with the minimal possible effort) may have led us to miss the earliest stage of colonization at the parcel scale. Alternatively, colonization of new parcels may have led to an explosive increase in the local population.

4.3. Spatial spread of water voles during parcel colonization

Parcel colonization spread in a northwest to southeast direction in a traveling wave, from *La Buffe* (a valley bottom more or less locked by the higher altitude areas of the *plateau d'Emparis* and the *Pic du Mas de la Grave* range) to the village of *La Grave*, then to the village of *Villar d'Arène*, and finally dying off at the *Col du Lautaret*. However, this spreading receded three times. The first time (from 1998 to 1999), it encountered the slopes of the *Mas de la Grave* range, which peaks at 3000 m. The second time, receding took place between two villages (from 2003 to 2004) and the third time in an area with deep gullies (from 2005 to 2006). Here, the inhabited areas and gullies appeared to be obstacles to the water vole spread, corroborating the findings of Berthier et al. (2013) in the Jura Mountains.

Traveling waves of water vole populations have also been studied in the Jura Mountains (Giraudoux et al., 1997; Berthier et al., 2013). Berthier et al. (2013) observed a spreading speed of 7.4 km per year in a northwest to southeast direction, radiating away from a major landscape discontinuity. In our study, the maximum annual distance covered was less than 4 km. Models indicate that landscape heterogeneities are instrumental in generating traveling waves because landscape heterogeneities impact vole dispersal (Sherratt et al., 2003; Johnson et al., 2004). When modeling large-scale landscape features, including absorbing boundaries (in which individuals who encounter obstacles perish), these models tend to show that the spatio-temporal dynamics of a colonization include perpendicular movement away from obstacles (Sherratt et al., 2003). This assumption is supported by our observation that water vole spreading in the Haute-Romanche valley receded three times after encountering obstacles, such as inhabited areas, gullies or steep slopes. In the Jura range, changes in water vole population abundance were monitored over 16 years (from 1989 to 2004) over a large area (>2500 km^2). Using graphical analyses and abundance data from an entire demographic cycle (from 1989 to 1994), Giraudoux et al. (1997) suggested that outbreaks emerge from epicenters located in a southwestern to northeasten strip of land and then spread as a traveling wave from the northwest to southeast over more than 2500 km^2 at a speed exceeding 10 km per year. In our study, we observed a similar process, in which colonization began very locally (i.e., the bottom of the *vallée de la Buffe*) and spread (but at a lower speed than that in the Jura Mountains). Berthier et al. (2013) demonstrated that this direction of the wave's movement (northwest to southeast) supports the idea that landscape obstacles generate a process similar to traveling waves. Similarly, the colonization of the Haute-Romanche valley occurred in a northwest to southeast direction, which was orthogonal to the potential obstacles surrounding the valley (i.e., peaks, forest, and gullies). Indeed, in the Jura Mountains, the water vole traveling wave also moved orthogonally to large-scale obstacles in the southeast and northwest; the waves' longitudinal axis was perpendicular to the direction of the waves (80–90°). In the Jura Mountain study, landscape discontinuities (e.g., subalpine mountain range, large forests, rugged terrain, lakes, and plowed land (Morilhat et al., 2007, 2008)) were unsuitable for water vole populations. Similarly to Giraudoux et al. (1997) and Berthier et al. (2013), we found that even on a comparatively small scale (10 km^2 against 2500 km^2), the traveling waves of water vole colonization were strongly shaped by natural (gullies, stiff slopes) and human (settlements) obstacles.

4.4. Impact of current land use and SLUT on water vole abundance during parcel colonization

Here, we show that the area of plowed fields, a habitat unfavorable to water voles (Morhilat et al., 2007), dramatically decreased in the Haute-Romanche between 1810 and 2003. This trend may explain the unimpeded spread of the water vole population along the valley, across the *La Grave* and *Villar d'Arène* villages. During this period, the amount of mown areas remained unchanged where the water vole colonization occurred. Mown areas are known to be more favorable to water vole populations (Morilhat et al., 2007). Furthermore, grazed parcels had lower water vole abundance during our study, which is consistent with previous findings reported by others (Morhilat et al., 2007). For instance, Morilhat et al. (2007) found that tramping by cattle and low grass height were highly unfavorable to water vole populations.

In our study, grazed parcels had lower water vole abundance than other parcels with any other land-use history. This finding indicates that land-use trajectories have no measurable effect on the water vole outbreak or colonization; instead, current land use appears to be the key-factor (e.g., the disappearance of plowed areas and the stability of mown areas where water vole outbreak occurred). The relationship between land use and topography may also drive water vole population spread. Valley bottoms, where the mown area remained stable and plowed in the past, have gentle slopes and relatively deeper soil, which is more favorable to water voles (Airoldi, 1976; Morilhat et al., 2007). In the Haute Romanche valley, topography and current land use can be assumed to be the main drivers of colonization, similar to patterns observed in the Jura Mountains (Berthier et al., 2013). By providing ample resources and shelter and by channeling vole dispersal, mown areas increase optimal habitat connectivity.

4.5. Origin of water voles

Girel et al. (2010) demonstrated that the landscape of the Haute-Romanche valley was already dominated by grassland in 1960. However no water vole outbreaks was reported until 1998. Actually, this outbreak coincides with the first record of the species in the valley. This finding is crucial because other areas in France where water vole outbreaks occur are also areas where water voles have been present for a long time (Butet and Spitz, 2001). This raises the question of where the first water vole colonizers came from. The species was known to be present in neighbouring valleys further north in Savoie. The genetic characterisation of populations and a phyllogeographic approach (Taberlet et al., 1998) would be essential to track the way the species may have colonized the Haute Romanche valley.

5. Conclusion

Recent land use changes in the Haute Romanche valley are characterized by the abandonment of plowing, the stabilization of mown areas at the valley bottom and the increase of grazed areas. Here, we describe the first colonization of a valley complex that was likely free of *A. terrestris* before 1998. This colonization shows similarities with the cyclic population variations reported in the Jura and the Massif Central Mountains, corroborating the idea that water vole colonization and outbreaks follow the same general pattern across regions. Our results corroborate earlier findings (Delattre et al., 1992, Giraudoux et al., 1997; Luque-Larena et al., 2013; Jareño et al., 2015) stressing about the role of historical changes of practice and landscape in triggering grassland small mammal outbreaks. This strengthens the notion that landscape management can be a way to regulate grassland small mammal populations. Parcel colonization followed a northwest to southeast gradient, and followed a pattern similar to that of traveling waves. We provide evidence that the spread receded three times, most likely due to the landscape structure. This finding illustrates the role of physical obstacles at the landscape scale. Finally, we showed that the driver of outbreak development is most likely to be current than historical land use. It appears that grazing limits the intensity of the outbreak and that, conversely, mown areas could be favorable to the water vole population, as they are in the Jura Mountains. Considering that mown areas are now being promoted by National and European Agri-Environmental Schemes to increase biodiversity, it may be important to promote spatial mosaic management for grasslands (e.g., a heterogeneous mosaic of mown, grazed and plowed areas, decreasing spatial connectedness) to take into account vole outbreak risks and biodiversity issues. However, such a management strategy may be difficult to organize, especially considering mowing in space and time, livestock grazing, etc. To develop a management scheme that takes these constrains into account will be a challenge for researchers, conservationists and farmers.

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