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Weak evidence of spatial segregation between the vulnerable southern water vole (*Arvicola sapidus*) and the two main invasive mammals of European freshwater ecosystems

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ABSTRACT

Niche differentiation by spatial segregation facilitates the coexistence of species sharing ecological preferences, which can buffer the impact of biological invasions on native species. The introduction of two semi-aquatic rodents, the coypu *Myocastor coypus* and the muskrat *Ondatra zibethicus*, to most freshwater ecosystems across Western Europe, has been pinpointed as a cause for the decline of the southern water vole (SWV) *Arvicola sapidus*. We investigated the co-occurrence of these three species in a river catchment of northwest France and whether spatial habitat segregation took place at two spatial scales, using hierarchical modelling accounting for imperfect detection. At a large spatial scale (river catchment), the occupancy rate of the SWV was 0.52 ± 0.06, i.e. noticeably smaller compared to coypu (0.58) and muskrat (0.80). We found no evidence of a negative effect of the presence of the two invasive rodents on SWV occurrence. At a smaller spatial scale (SWV home range), we found weak evidence of spatial segregation in habitat use with a negative, although not significant, effect of muskrat. Overall, our results suggest that riparian habitats in the study area allow the southern water vole to coexist with two larger invasive rodents, provided that hygrophytic vegetation is preserved alongside rivers.

RÉSUMÉ

La différenciation des niches par ségrégation spatiale est un processus qui facilite la coexistence d'espèces partageant les mêmes préférences écologiques. Ce processus peut atténuer l'impact des invasions biologiques sur les espèces natives. L'introduction de deux rongeurs semi-aquatiques, le ragondin (*Myocastor coypus*) et le rat musqué (*Ondatra zibethicus*), dans la plupart des écosystèmes d'eau douce d'Europe occidentale, a été identifiée comme une cause du déclin du campagnol aquatique (*Arvicola sapidus*). A l'aide de modèles hiérarchiques tenant compte de la détection imparfaite des espèces, nous avons étudié à deux échelles spatiales différentes la co-occurrence de ces trois espèces dans un bassin hydrographique du nord-ouest de la France. Nous avons cherché à déterminer s'il existait un phénomène de ségrégation spatiale entre les 3 espèces. À large échelle (bassin versant), le taux d'occupation du campagnol aquatique est de 0,52 ± 0,06, c'est-à-dire sensiblement plus faible que celui du ragondin (0,58) et du rat musqué (0,80). Nous n'avons trouvé aucune preuve d'un effet négatif de la présence de ces deux rongeurs envahissants sur l'occurrence du campagnol aquatique. À plus petite échelle (territoire du campagnol aquatique), nous avons trouvé une faible preuve de ségrégation spatiale dans l'utilisation de l'habitat avec un effet négatif, bien que non significatif, de la présence du rat musqué. Dans l'ensemble, nos résultats suggèrent que les ripisylves de la zone d'étude permettent au campagnol aquatique de co-exister avec deux rongeurs envahissants de taille supérieure, à condition que la végétation hygrophile soit préservée le long des rivières.

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Introduction

Niche differentiation represents a process allowing species to cope with competitively superior species (Harrington et al. 2009), and in particular with introduced competitive species. Indeed, the introduction of an alien species does not systematically lead to competitive exclusion of native species (Cayuela et al. 2013). Niche differentiation involves three non-mutually exclusive dimensions: spatial, temporal and trophic (Pianka 1969; Case and Gilpin 1974; Albrecht and Gotelli 2001; Wereszczuk and Zalewski 2015), with spatial habitat segregation being the most frequent (Schoener 1974). Spatial habitat segregation is therefore identified as an important mechanism to facilitate the coexistence of species sharing similar resources. Competition for resources decreases when species use different parts of a same area, either spatially or

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temporally (Pita et al. 2010). Species coexistence is a scale-dependent process: coexistence at the large regional scale of the community may be facilitated by spatial segregation at a smaller, local scale (Patterson and Brown 1991; Brown et al. 2000; Amarasekare 2003; Pita et al. 2016). Conditions for coexistence between native and invasive species have received relatively little attention so far (Peters and Lodge 2013). However, it seems essential to understand the mechanisms leading to species coexistence and to identify the spatial scale at which these processes occur, in order to implement the appropriate management measures in a context of invasion.

When alien species are introduced into a new environment, they can alter the organisation and functioning of ecosystems (Vilà et al. 2010; Pyšek and Richardson 2010) through various processes such as predation (Woodroffe et al. 1990; Bryce et al. 2011), parasite and disease transmission (Dunn et al. 2009), hybridization (Huxel 1999) and competitive exclusion (Byers 2000), which may ultimately lead to the extinction of native species (Mooney and Cleland 2001). Buffering the potential impact of biological invasions is challenging and requires the identification of the process by which native species are impacted (Mooney and Cleland 2001; Ricciardi 2003; Rouget et al. 2016). Competition with native species is one of the most common consequences of alien species' introduction (Cadi and Joly 2004; Violle et al. 2011). Many studies have indeed shown that successful invasive species are competitively superior to native species (Heard and Sax 2013).

The southern water vole *Arvicola sapidus* (Miller 1908; hereafter SWV) is a native semi-aquatic rodent occurring in freshwater habitats in parts of France, Spain and Portugal. Its distribution and habitat selection are mostly determined by the combined presence of freshwater, food and vegetation cover (Bonesi et al. 2002). SWV populations are declining in a large part of its distribution and therefore this species is classified as vulnerable in the Red List of Threatened Species (IUCN 2017). The decline of SWV populations is mostly due to the destruction and fragmentation of its habitat (Pita et al. 2013; Grilo et al. 2018) and predation by an invasive predator, the American mink *Neovison vison* (Melero et al. 2012; García-Díaz et al. 2013). Grey literature also suggests the impact of competition with other invasive species such as the coypu (*Myocastor coypus* Molina) and the muskrat (*Ondatra zibethicus* L.) (e.g. Rigaux 2015) but to our knowledge no formal scientific studies have confirmed this. Muskrat and coypu, two semi-aquatic rodents, were introduced in Europe between the late 19th-early 20th centuries for fur trade. In France, individuals were released into the wild following farm closures, and the two species rapidly colonised most of the territory, during the 1940s-1950s for muskrat and 1960s-1970s for coypu (Maurin and Gavazzi 1997). Their ecological plasticity facilitated their expansion over a wide range of freshwater and brackish ecosystems across Europe, where their excavation activities alter riverside ecosystems (Carter et al. 1999; Manchester and Bullock 2000).

About sixty years after colonisation by coypu and muskrat, very little is known about the current impact of these two invasive aquatic rodents on the SWV. Coexistence of these species has been recorded, suggesting that processes such as spatial habitat segregation (i.e. niche differentiation) may have taken place. Here we tested for the occurrence of niche differentiation between SWV and the two larger-bodied aquatic rodents at two nested spatial scales in a large river catchment of northwest France (2,300 km^2). Specifically, we conducted a site-occupancy survey, accounting for imperfect detection, to assess the SWV distribution in relation with the presence of invasive species and riparian habitat characteristics at the catchment scale. Then, in each cell occupied by SWV, we further explored the pattern of spatial co-occurrence between species at the scale of a rodent home range.

Material and methods

Study species

Weighting up to 280 g, the southern water vole is the largest vole of Europe. It is considered highly dependent on freshwater (Garde and Escala 2000), although the species may be found in dry streams, ponds, irrigation ditches and wetlands, sometimes far from main water bodies (Fedriani et al. 2002; Pita et al. 2010). Its main habitat consists of tall and dense herbaceous vegetation patches dominated by a hygrophilic plant community (Fedriani et al. 2002; Pita et al. 2010; Peralta et al. 2016). Generally, SWV colonies comprise between 6 and 31 individuals (mean ± 1 SD: 19 ± 8; Centeno-Cuadros et al. 2011) distributed over a suitable patch of 80–150 m long (Rigaux et al. 2009), with a strong site fidelity. The home range size depends on habitat quality (mean size of 946 ± 28.2 m^2 [Pita et al. 2010]; 2615 ± 801 m^2 for individuals with stable home range [Mate et al. 2016]).

Originating from North America, the muskrat is a semi-aquatic rodent that weights from 0.9 to 1.36 kg (Donohoe 1966). This species colonised northwest France in the 1940s (Maurin and Gavazzi 1997) and is currently present in a wide variety of semi-aquatic habitats such as ponds, rivers, lakes, streams, irrigation canal and road ditches (Bourget 2010). The home range of muskrats spans over 582 ± 56 m of riverside with

a using space aggregated around established burrows (Ahlers et al. 2010). Native from South America, the coypu is a large semi-aquatic rodent (6.5–10 kg) which colonized northwest France in the 1970s (Maurin and Gavazzi 1997) and lives in similar habitats to those used by muskrats (Baroch et al. 2002). Rarely observed further than 100 m away from rivers (Bertolino et al. 2005), coypus have home ranges varying from 2 to 5 ha (up to 12 ha) and can travel distances between 40 m and 1.25 km per day, although most do not go further than 400 m a day (Micol et al. 1996).

Study area

We conducted this study in the Risle river catchment, located in northwest France (49.095°N 0.566°E EPSG: 4326; Figure 1). The catchment area of this river and its major tributary, the Charentonne, covers an area of 2,300 km^2. The Risle river runs for 210 km before joining into the Seine River. With a total of 36 secondary tributaries, the catchment area comprises almost 760 km of permanent rivers and streams. This area is characterized by oceanic climate with moderate precipitations well distributed over the year (ca. 170 rainy days). Nevertheless, the average annual rainfall varies from 840 mm per year in the west to 620 mm in the east. The upstream of the river is made of impermeable soils (marls, hard limestone, sandy or siliceous clays), inducing sudden change in flow rate in this area following rainy events (SAGE Risle et Charentonne 2005). The downstream of the river has on the other hand a porous substrate, ensuring a more regular flow. Riversides of the Risle and its tributaries are relatively well preserved and mainly constituted of permanent pastures and wetlands areas. The riparian woodland is mostly discontinuous and narrow with denser patches occurring along small tributaries.

Field procedures and survey protocols

The permanent natural (streams, rivers) and artificial (ponds) water bodies occurring in the study area were represented into a random-origin grid of 606 cells of 1 × 1 km using Quantum GIS v.2.14.3 (QGIS Development Team 2016), among which 150 cells were randomly selected for surveying (Figure 1). A further selection was conducted using aerial photographs to exclude cells with unsuitable areas for SWV, defined as dense riparian woodland and urbanised areas without riparian vegetation. During the first field prospection in March 2016, hygrophilic riparian vegetation, i.e. the suitable habitat for SWV (Pita et al. 2011, 2013), was searched for in every selected cell. If no suitable habitat was found in a cell, the latter was no longer prospected

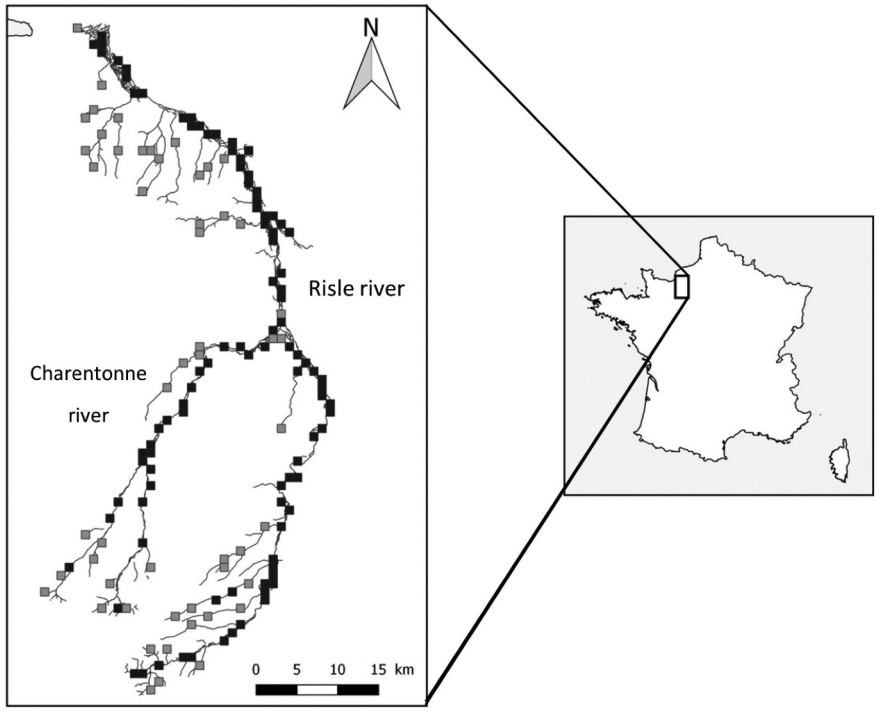

Figure 1. Study area in the Risle river catchment in northwest France, and its major tributary, the Charentonne river. The stream network is indicated in grey. Squares represent random site selection with black squares indicating patches with favourable habitat used in the survey (N = 98). Grey squares indicate patches of unsuitable habitat that were excluded from the survey (N = 52).

and was excluded from the dataset. Within each selected cell (N = 98, 16.2% of the study area), a 100 m-long transect (hereafter 'site') was surveyed on the riverside judged as the most favourable for the SWV (same transect length as used by the SWV French National Survey [Rigaux 2015]). A visual cue was positioned (and recorded with GPS) at the beginning of each site to ensure the same site was surveyed at every visit. A unique, previously trained, observer (EL) meticulously waded along the transect, seeking for faeces for 35 minutes within 2 m from the riverside. Faeces of the SWV (Fedriani et al. 2002; Mate et al. 2013; Pita et al. 2013) are easily distinguishable from the two invasive species (Rezendes 1999) thanks to their colour and size and therefore provide a reliable method for recording SWV presence. Transect survey was stopped as soon as faeces of the three species were found. The same observer visited each site at three occasions in 2016, between 16 March and 14 May, i.e. during the SWV breeding season where patch occupancy can be assumed constant (for all species). Visits were at least 2 weeks apart to minimise observer bias due to memory effect. We assumed that no site colonisation or extinction occurred during the survey (breeding) period.

Detection probability varies spatially due to site-specific habitat characteristics patterns and temporally in relation to breeding behaviours and changing environmental conditions (Bailey et al. 2004). Surveys were not conducted during heavy rains as they reduce faeces detection (Fusillo et al. 2007). We recorded rainy events occurring within the last three days preceding the survey (*Rainfall*, a binary variable) to account for its effect on detectability. Other survey-specific covariates included date of prospection (*Date*: we used Julian date with day 1 = March 16), the height of riparian vegetation (*Veg_h*: <30 cm or ≥30 cm, a binary variable) and the water level in the river (*Water_rise*: 0/1, a binary variable). For the former parameter, it has been defined that *Water_rise* = 1 when the water level was above the riparian vegetation (>10 cm) at least in part of the transect. As the vegetation height was sufficiently homogeneous along the whole site for only one of the two categories (< 30 cm or ≥ 30 cm) to be represented, only one measurement of this binary variable was made.

In order to characterize the habitat of SWV, in addition to vegetation hight (*Veg_h*) we measured site-specific covariates potentially relevant for occupancy alongside a 100 m-long transect. We collected data on the type of the most representative riparian vegetation located within 2 m from the riverside (*Veg_type*) at each site: mesophilic or hygrophilic plants, woody vegetation. Vegetation height (*Veg_h*) was used to model both detection and occupancy of SWV. At each site, percentage of cover by aquatic vegetation (*Veg_co*) was visually estimated on the whole transect using four vegetation cover classes: 0, 1–25%, 26–50% and 51–100%. Vegetation cover might positively affect the capacity of SWV to move alongside the river. From aerial photos taken in 2012–2015, we estimated river width (*River_w*) on QGIS, from an average over 10 points located at equal intervals alongside the transect.

As our intent was also to determine if the presence of SWV was affected by the presence of invasive species (muskrat and coypu), while accounting for habitat features, we assessed the use of a particular site by the invasive rodents (*D_Onda; D_Myo*) on a scale ranging from 0 to 3, based on the number of detections after three occasions. This covariate was also altered into presence-absence data (species-specific presence: *P/A_Onda; P/A_Myo*; presence of at least one invasive rodent: *P/A_inv*).

As a second step, we assessed whether spatial segregation in habitat use between the three species occurs at small spatial scale (SWV home range). To achieve this, we selected, among the 98 sites surveyed for the large-scale protocol those with both SWV and at least one of the two invasive species detected during at least two occasions (N = 27). Each original transect was lengthened to 200 m and subdivided into 10 segments of 20 m long that constituted the adjacent spatial replicates. Each segment was sampled only once (between 15 June and 30 June) for 10 minutes, by the same observer to detect faeces of SWV, muskrat and coypu. Presence of muskrat ($P/A_{_Onda}$), presence of coypu ($P/A_{_Myo}$), presence of any of these two species: 0 or 1 ($P/A_{_inv}$) and species richness of invasive species: 0, 1 or 2 ($Rich_{_inv}$), were treated as categorical variables. In each segment, we also characterised the herbaceous plant type (mesophilic or hygrophilic) and the height (≥30 cm) of riparian vegetation located between 0 and 0.5 m (*Veg_type1; Veg_h1*) and 0.5–2 m (*Veg_type2_H; Veg_h*2) from the riverside and presence of wood between 0.5–2 m (*Veg_type2_W*). Local scale surveys were always carried out in periods without precipitation over the last three days. Only 18 sites of the 27 original ones were surveyed because of accessibility issues (reluctant landowners, development of dense thorns). The same observer visited every segment in June 2016. Two of these 18 sites were excluded following the important deterioration of the riverside vegetation due to intensive browsing by cows; the final dataset included 16 sites.

Statistical procedures

For analysing the large-scale survey, we used hierarchical occupancy models to estimate SWV occupancy

probability in relation to habitat features and occurrence of invasive species (MacKenzie et al. 2002). We modelled the probability of detection p and occupancy rate ψ using single-season occupancy models with Program PRESENCE v.11.0 (Hines 2010). Model assumptions were that (1) occupied sites remain occupied for the duration of the survey, (2) the species is not detected when absent (i.e. no false positive), and (3) detection at one site is independent of detection at all other sites (MacKenzie et al. 2002). The probability of detecting the invasive species at least once over three surveys was very close to 1 (see results), such that a multi-species occupancy modelling approach would have brought only little added value but too many parameters given the sample size available.

First, we explored the effects of different covariates on detectability, using a full parameterisation for occupancy (*P/A_inv* + *Veg_h* + *Veg_co* + *Veg_type* + *River_w*). Models were run with detectability set as a function of *Date, Rainfall, Veg_h, Water_rise* (all additive combinations tested). We selected the best detectability model based upon the Akaike Information Criterion (AIC; Burnham and Anderson 2004). This parameterisation was then held constant while a similar model selection procedure was performed regarding occupancy. Occupancy was modelled as a function of habitat features and presence of invasive species: *Veg_type, Veg_h, Veg_co, River_w, D_Onda, D_Myo, P/A_Onda, P/A_Myo, P/A_inv*. All combinations of additive models were tested, with a maximum of 5 covariates for occupancy, keeping the ratio N/K ≥ 10 (N: sample size, K: number of parameters used in the model). Moreover, the sum of AIC model weights for every covariate was calculated to demonstrate the influence of each covariate (Burnham and Anderson 2004). Similar models (intercept only) were run for both the coypu and the muskrat to derive species-specific p and ψ.

The sampling design used at a local spatial scale involved a component of spatial dependency between replicates (segments). To account for non-independence in the data, we used the recently developed Markovian occupancy models designed for spatially adjacent replicates (Hines et al. 2010). This model estimated four parameters: p, the probability of detecting the SWV in a segment conditional on the presence of the species on the site; ψ, the probability that a site is occupied or used by a species; *00*, the probability that a species is present on a segment given that the site is occupied but the species was absent on the previous adjacent segment; and *01*, the probability that a species is present on the segment given that the site is occupied and that the species was present on the previous adjacent segment (Hines et al. 2010; Karanth et al. 2011; Charbonnel et al. 2014, 2015). Surveys based on adjacent spatial replicates along streams and the Markovian occupancy model parameter settings are adequate for a species with a small and linear home range (Charbonnel et al. 2014). In the sampling design, each segment was sampled only once, such that we assumed $p = 1$ for every segment. We tested the influence of each covariate (*Veg_type1, Veg_type2_H, Veg_type2_W, Veg_h1, Veg_h*2, *P/A_Onda, P/A_Myo, P/A_inv* and *Rich_inv*) on ψ. Model selection procedure was similar to previously described. Estimates are presented as mean ± SE.

Results

Southern water vole habitat and species co-occurrence at a catchment spatial scale

The southern water vole was detected at least in one of the three occasions in 47 of the 98 cells sampled and the occupancy rate, accounting for imperfect detection, averaged 0.52 ± 0.06. Detectability of the SWV averaged 0.73 ± 0.04 (95% CI = [0.64; 0.80]) per occasion. Over three occasions, the cumulated probability of detection of the species reached 0.98. Detectability decreased with survey date (effect size β = –-0.034 ± 0.012 per day on logit scale). For an average survey date (day = 33.6), detectability following the rise of the river level decreases from 0.77 to 0.05. We did not find evidence for an effect of rainfall or vegetation height on the detectability of the SWV (Table 1). The two invasive species showed higher occupancy rates with 0.80 ± 0.04 and 0.58 ± 0.05 for the muskrat and the coypu, respectively (Figure 2). The probability of detecting a coypu or a muskrat at least once over three surveys was very close to one: 0.97 and 0.99, respectively.

Among the habitat covariates tested for occupancy, the best model retained vegetation height and river width (Table 2). Specifically, vegetation height on the river side was also highly influential with occupancy rate rising from ψ = 0.08 when it was shorter than 30 cm, to ψ = 0.74 when it was higher than 30 cm (Figure 3). Secondarily, larger parts of the river tended to host SWV more often (β = 0.69 ± 0.34 on logit scale; Figure 3).

SWV occupancy was not affected by the presence of neither of the two invasive aquatic rodents (coypu or muskrat; Figure 2). This result held true considering the presence of either species ('invasive' considered as present when at least one species was present), the presence of each species separately (two-level factors) or the sum of detection over the three surveys (a proxy of habitat uses for each species separately).

Table 1. Results of the model selection regarding the detection probability *p* and the probability of occurrence (*ψ*) of the Southern water vole. The number of parameters contributing at the model (k), the Akaike Information Criterion (AIC), the Delta AIC (Δ AIC) (i.e. the difference in AIC between focal and best models). To estimate the probability of detection, the probability of occurrence (*ψ*) for all models was held constant: *ψ*(*P/A_inv* + *Veg_h* + *Veg_co* + *Veg_type* + *River_w*). To model the occupancy propability, the detection probability (p) was held constant (with the best parameterisation found *p*(Date+*Water_rise*). Only a subset of models are shown.

Model specification for detectability *p*	k	AIC	Δ AIC
Date + Water_rise	9	248.44	0.00
Date + Water_rise + Veg_h	10	248.69	0.25
null model	7	275.35	26.91
Model specification for occurrence *ψ*	k	AIC	Δ AIC
Veg_h + River_w	**6**	**243.38**	**0.00**
P/A_Onda + Veg_h + River_w	7	244.17	0.79
D_Myo + Veg_h + River_w	7	244.90	1.52
P/A_Myo + Veg_h + River_w	7	245.17	1.79
D_Ond + Veg_h + River_w	7	245.21	1.83
P/A_inv + Veg_h + River_w	7	245.35	1.97
P/A_Onda + P/A_Myo + Veg_h + River_w	8	245.56	2.18
P/A_inv + Veg_h + Veg_type + River_w	8	246.34	2.96
D_Onda + D_Myo + Veg_h + River_w	8	246.61	3.23
P/A_inv + Veg_h + Veg_co + Veg_type + River_w	9	248.23	4.85
null model	4	271.12	27.74

Note: Date of occasion (Date), rainfall during the survey day or the three days preceding the survey (Rainfall), height of riparian vegetation (*Veg_h*) and water level in the river (Water rise), vegetation height (*Veg_h*), vegetation type (*Veg_type*,), aquatic vegetation cover (*Veg_co*), river width (*River_w*), presence/absence of muskrat (*P/A_Onda*), presence/absence of coypu (*P/A_Onda*), presence/absence of invasive species (*P/A_inv*), use of habitat by coypu (*D_Onda*), use of habitat by muskrat (*D_Myo*).

Patterns of habitat use of the three aquatic rodents at a small spatial scale

On the 16 sites selected to evaluate a potential spatial segregation at a local scale between SWV and the two invasive species, muskrat was ubiquitous (all sites), and coypu was detected at 10 sites. Muskrat was detected at 102 out of the 160 segments (63.8%), while SWV was detected at 74 (46.3%) and coypu at 62 (38.8%).

We compared the relative performance of a set of plausible alternative models for SWV habitat use. For the 7 models showing a difference in AIC ≤ 2, a common structure with 3 covariates (*Veg_type1, Veg_h1, Veg_h*2) was retained (Table 2). The sum of AIC model weights for every covariate also indicated that these covariates were the most relevant for explaining SWV occupancy (Figure 4). These models suggested that habitat use by SWV was positively influenced by the riparian vegetation height (*Veg_h*2), specifically between 0.5 and 2 m of the riverside (from the best model: $\beta = 2.13 \pm 0.86$, on logit scale; Figure 4). SWV occupancy increased when the height of the riparian vegetation between 0 and 50 cm (*Veg_h1*) was greater than 30 cm ($\beta = 1.99 \pm 0.92$). Habitat use of SWV was affected by type of riparian vegetation between 0 and 50 cm (*Veg_type1*) of the riverside with a decrease of occupancy when vegetation was mesophilic ($\beta = -1.75 \pm 0.61$) compared with a hygrophilic vegetation. The most parsimonious model (Table 2) also included the presence of muskrat, but the decrease in AIC was marginal compared to the second-best model with the three habitat variables only (ΔAIC = 0.06). At this small spatial scale, the presence of muskrat tended to decrease SWV habitat use, though not significantly ($\beta = -1.12 \pm 0.83$).

Discussion

The occurrence of SWV was primarily dependent upon the presence of hygrophilic vegetation on the very edge of the river. We found no clear evidence for a competitive exclusion process operating at either small (species home range) or large (river catchment) spatial scales. While we cannot rule out the negative impact of the large-bodied rodents on SWV during the early phase of the invasion phase in the second half of the 20th century, the three species seem to currently coexist in riparian habitats of northwest France.

Riparian habitats and occurrence of the Southern water vole

At both large (catchment) and small (home range) spatial scales, SWV occurrence/habitat use was primarily influenced by the type and height of the riverside vegetation. These results are consistent with previous studies (Pita et al. 2011; Mate et al. 2013; Peralta et al. 2016). SWV is considered as a specialist of habitats with dense hygrophilic vegetation (Pita et al. 2011; Mate et al. 2013, 2016) with *Juncus* spp., *Carex* spp., *Phragmites* spp. and *Typha* spp. This permanent vegetation cover provides food resources, shelter from predators as well as nesting sites (Barreto et al. 1998; Fedriani et al. 2002; Mate et al. 2013; Peralta et al. 2016). As Fedriani et al. (2002), we found that patches with such vegetation cover ≥ 30 cm tall provide suitable sections of riverside for SWV. At the spatial scale of the river catchment, we found quite unexpectedly that SWV was slightly more likely to occur alongside large rivers (mean river width in the area: 5.7 ± 6.0, range: 0.6–26.4 m). This finding contradicts previous results from a survey conducted at the national level in France and showing that the species was slightly more likely to be found alongside rivers of 0.5–1 m wide (Rigaux 2015). Two hypotheses could explain this discrepancy. First, narrow rivers in our

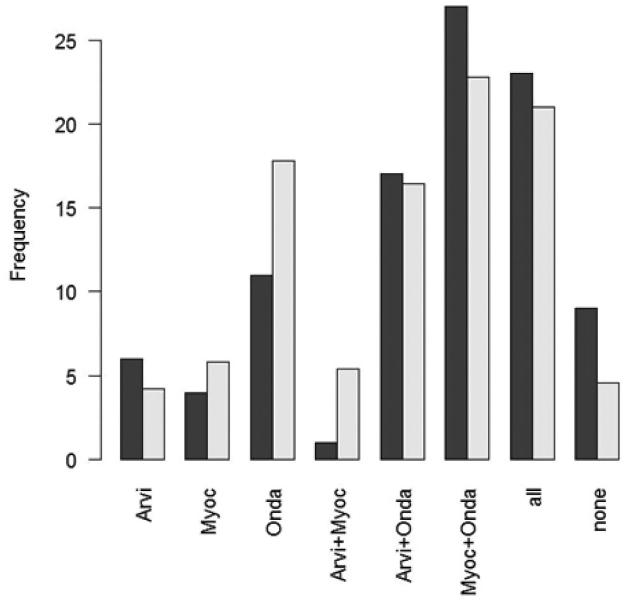

Figure 2. Observed (dark bars) vs. expected (light bars) species occurrence and co-occurrence (number of sites) of the three aquatic rodent species: southern water vole (*Arvi*), coypu (*Myoc*) and muskrat (*Onda*). The expected frequencies were derived from the specific average occupancy rates ψ. Total number of sites surveyed was 98.

catchment mainly occur upstream and typically show extensive riparian woodland areas at the expense of dense herbaceous riverbed, due to competition for light (Ricard and Messier 1996). Second, upstream rivers occur on more impermeable soils compared to downstream and concentrate small hydraulic structures (ca. 400 hydraulic structures in the catchment area) causing important and rapid fluctuations of water level (SAGE Risle et Charentonne 2005), that can lead to the flooding of SWV burrows (Carter and Bright 2003). Many aquatic and semi-aquatic species have evolved with annual flood pulses and are able to adapt to seasonal and cyclic changes in river flows (Sparks 1995). Nevertheless, extreme fluctuations in water levels caused by river management can have both direct and indirect negative impacts on those species (Alho and Silva 2012). Direct impacts involve burrow flooding that can cause litter drowning and force individuals to move in sub-optimal habitats where they might become more vulnerable to predators (Moorhouse et al. 2009).

Coexistence of native and invasive semi-aquatic rodent species

At large spatial scale, we did not detect any negative effect of invasive species on SWV. The three species seem to coexist at the scale of a river catchment in northwest France, with a relatively high level of patch occupancy (0.52, 0.80 and 0.58 for SWV, muskrat and coypu, respectively). We further tested whether this coexistence at the large-scale could be the result of a spatial segregation operating at the home-range level. The spatial segregation in habitat use may be measurable as a reduced occupation probability by one species when the other is present (Amarasekare 2003; Fisher et al. 2013). However, we only found a weak support for this hypothesis, the presence of muskrat retained in the best model showing a negative but not significant effect on SWV habitat use. However, this analysis may suffer from reduced statistical power as the occupancy of adjacent segments was surveyed only once. Imperfect detection tends to underestimate the effect of covariates (Tyre et al. 2003). SWV territories can overlap both with those from conspecifics and with other rodents species (Pita et al. 2010). Our test of spatial segregation occurred over a month in a single year, and we cannot therefore exclude the possibility of stronger segregation during another season (South 1999) or in years with reduced food availability (Andrzejewski and Mazurkiewicz 1976). A telemetry study conducted on both SWV and muskrat could provide additional information on a potential spatial segregation (Benson and Patterson 2013). Coexistence of species sharing similar resources can be possible if the overall carrying capacity of the environment is not reached (Sayre 2008). Here, SWV, muskrat and coypu consume overall, the same food resource consisting of hygrophilic vegetation. Our sampling design was focused on suitable habitats for SWV (i.e. dense herbaceous vegetation). In such optimal habitats, spatial segregation appeared to be weak,

Table 2. Results of the Markovian occupancy model selection regarding the probability of occupancy ψ of the water vole using Akaike Information Criterion (AIC), Delta AIC (ΔAIC) and number of parameters (k). The detection probability p for all models was held constant with p(.) and ψ(.), 00(.), 01(.), p(.) represents the null model. Best model in bold. Only a subset of models are shown.

Model specification for occupancy ψ	k	AIC	Δ AIC
Veg_type1+ Veg_h1+ Veg_h2 + P/A_Onda	**8**	**149.81**	**0.00**
Veg_type1+ Veg_h1+ Veg_h2	7	149.87	0.06
Veg_type1+ Veg_type2_H+ Veg_h1+ Veg_h2	8	150.38	0.57
Veg_type1+ Veg_h1+ Veg_h2+ Rich_inv	8	151.30	1.49
Veg_type1+ Veg_type2_W+ Veg_h1+ Veg_h2	8	151.35	1.54
Veg_type1+ Veg_h1+ Veg_h2 + P/A_Myo	8	151.61	1.80
Veg_type1+ Veg_h1+ Veg_h2 + P/A_inv	8	151.81	2.00
Veg_type1+ Veg_type2_H+ Veg_h2 + P/A_Onda	8	152.92	3.11
Veg_type1+ Veg_h2 + P/A_Onda	7	153.70	3.89
Veg_type1+ Veg_h1	6	154.26	4.45
Veg_type1+ Veg_h1+ Rich_inv	7	154.52	4.71
null model	4	195.24	45.43

Note: Vegetation type of riparian vegetation located between 0–50 cm from the riverside (*Veg_type1*), herbaceous type of riparian vegetation located between 50 cm-2 m from the riverside (*Veg_type2_H*), presence of wood on riparian vegetation located between 50 cm-2 m from the riverside (*Veg_type2_W*), height of vegetation of riparian vegetation located between 0–50 cm from the riverside (*Veg_h1*), height of riparian vegetation located between 50 cm-2 m from the riverside (*Veg_h*2), presence of muskrat (*P/A_Onda*), presence of coypu (*P/A_Myo*), presence of any of these two species (*P/A_inv*) and species richness of invasive species (*Rich_inv*).

possibly because the carrying capacity is sufficient to meet the needs of the three species. Whether SWV suffers more from the competition with muskrat and coypu in sub-optimal habitats, therefore limiting its potential distribution, remains to be assessed.

Our results show weak, if any, spatial segregation between the two invasive species and the SWV, whatever the spatial scale considered. However, this finding does not mean that coypu and muskrat have not induced in the past a shrinkage in the distribution and abundance of the SWV. Indeed, invasive species impact native communities through different processes alongside the successive phases of colonisation, establishment, spread and equilibrium, the first three ones being the most deleterious (Salo 2005; Ricklefs 2008). The contemporary situation may reflect a new stable equilibrium, with the native species occurring at a much lower density than before the invasions. For instance, Ruffino et al. (2009) showed that, at the regional scale, black rat (*Rattus rattus*)

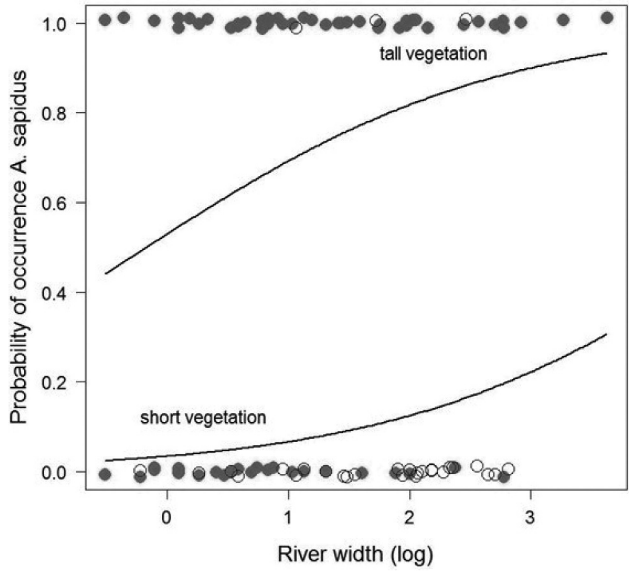

Figure 3. Probability of occurrence of the southern water vole at the catchment scale according to log-transformed river width, derived from the best occupancy model (ψ (*Veg_h* + *River_w*), see Table 1), accounting for detectability (p (Date + *Water_rise*)). Grey and open circles correspond to tall (> 30 cm) and short (< 30 cm) riparian hygrophytic vegetation. A small jitter has been added on the y-axis to improve the visibility of data points.

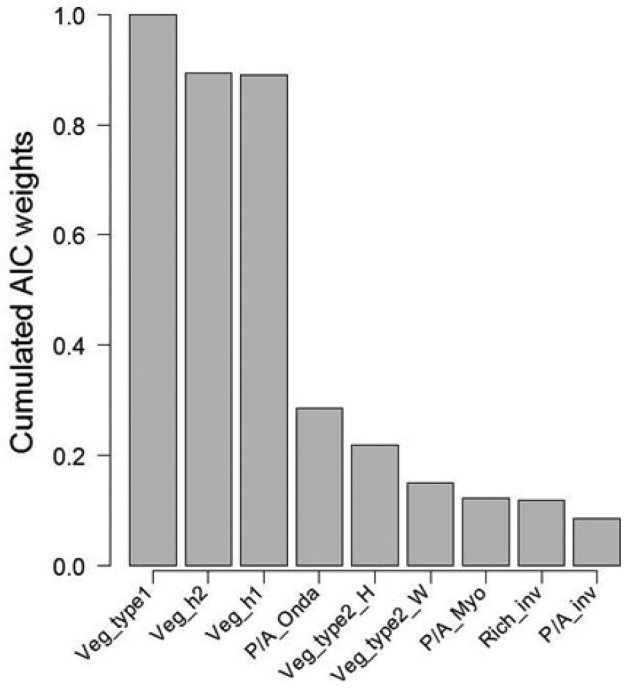

Figure 4. Sum of AIC model weights for each of the covariates used in the modelling of the probability of habitat use by the SWV (small spatial scale). Covariates considered here were: vegetation type of riparian vegetation located between 0–50 cm from the riverside (*Veg_type1*), herbaceous type of riparian vegetation located between 50 cm-2 m from the riverside (*Veg_type2_H*), presence of wood on riparian vegetation located between 50 cm-2 m from the riverside (*Veg_type2_W*), height of riparian vegetation located between 0–50 cm from the riverside (*Veg_h1*), height of riparian vegetation located between 50 cm-2 m from the riverside (*Veg_h2*), presence of muskrat (*P/A_Onda*), presence of coypu (*P/A_Myo*), presence of any of these two species (*P/A_inv*) and species richness of invasive species (*Rich_inv*).

presence was only a limiting factor in the abundance of the smallest seabird, the storm petrel (*Hydrobates pelagicus*), while the distribution and abundance of three large-bodied shearwaters were more influenced by island characteristics in the Mediterranean. However, a rat removal experiment conducted on a Tunisian island showed an immediate increase in breeding numbers of Scopoli's shearwater (*Calonectris diomedea*), demonstrating that in the apparent equilibrium previously observed, the native species was kept at very low density by invasive rats (Bourgeois et al. 2013). Many removal programs are currently conducted on muskrat and coypu throughout France and looking at their impact on SWV populations, in a properly designed experiment, would be insightful for optimising conservation actions on riparian ecosystems.

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