Streams and adjacent riparian habitats represent linked terrestrial and aquatic ecosystems that exchange materials and energy. Recognized relationships among apex predators and ecosystem biodiversity led us to hypothesize that these predators in riparian-stream systems were more likely to be found in sites with high stream quality, defined as increased ecosystem function and integrity. In our freshwater study system, river otter *Lontra canadensis* and mink *Neovison vison* play critical roles as apex predators. We used multi-season occupancy modelling across three sampling years (2012–2014) to compare aspects of the stream communities that explain occupancy dynamics of river otter and mink, including their interactions with other semi-aquatic mammals. We surveyed for semi-aquatic mammals at 77 sites in 12 major watersheds in southern Illinois, USA (44 526 km²). Naïve occupancy differed among years but generally increased for river otter, and remained high (≥93.5%) for mink. Increasing substrate availability increased detectability of river otter, whereas mink detection varied by survey period. Occupancy of river otter during the initial survey period was higher in sites closer to reintroduction points. Probability of colonization of river otter was positively associated with macroinvertebrate index of biotic integrity, fish species richness, and beaver presence. Sites with high species richness of fish families preferred by river otter also had increased river otter persistence. Mink occupied sites with increased fish richness, muskrat presence and mussel community index. Taken together, our results show occupancy of both mink and river otter were predicted by aspects of prey diversity and presence, indicating the importance of community composition in occupancy dynamics of riparian predators. Ultimately, these relationships suggest that habitat heterogeneity and system stability are important to apex predator site use. However, the relative role of bottom–up and top–down forcing in stream systems remains to be resolved.

Keywords: community ecology, trophic interactions, semi-aquatic mammals
Introduction

Streams and adjacent riparian habitats represent unique systems where materials and energy are exchanged between terrestrial and aquatic ecosystems (Likens and Bormann 1974, Hynes 1975, Baxter et al. 2005). The effect of changes within watersheds (e.g. land use, reduction of riparian areas; Allan 2004, Heatherly et al. 2007, Sweeney and Newbold 2014) on water quality and stream (aquatic) communities is well-studied, but relationships between stream quality, defined as increased ecosystem function and integrity, and riparian fauna (particularly predators) are poorly understood (but see Bennett 2014). The presence of an apex predator within a system can have far-reaching effects via top–down controls and trophic cascades (Gittleman and Gompper 2005, Roemer et al. 2009) that can alter disease rates, ecosystem metabolism, and biodiversity (Estes et al. 2011). We were interested in elucidating the relationship between stream quality and site use by semi-aquatic carnivores, specifically comparing the relative importance of community diversity at multiple trophic levels, prey availability and interactions with other semi-aquatic mammals.

Biotic indicators of stream quality are likely to be predictive of the quantity and types of prey available for riparian predators. Stream quality is assessed using biological indicators at all taxonomic levels, accounting for changes in the physical and chemical aspects of the stream as well as short- or long-term disturbances (Rosenberg and Resh 1993). Macroinvertebrate communities vary predictably with land-cover and nutrient concentrations (Heatherly et al. 2007), leading them to be widely used as biological indicators of stream quality (Rosenberg and Resh 1993). For instance, declining mussel biodiversity has been linked to decreased stream quality due to changing land use (Poole and Downing 2004). The use of macroinvertebrates to assess stream quality is further bolstered by their importance to ecosystem functions such as decomposition, and they can propagate both bottom–up and top–down processes because they tend to occupy middle trophic levels and contribute to subsidy fluxes (Wallace and Webster 1996, Baxter et al. 2005). Fish communities also are used as indicators of stream quality, as changes to water conditions and land use can alter food resources and communities at higher trophic levels (Karr 1981, 1991, Fierro et al. 2017).

Species richness and diversity are often considered indicators of habitat quality (Karr 1991, Rosenzweig 1995), and also may represent an index of long-term prey availability for riparian predators. Community stability may increase with increased species diversity due to increased food web linkages (MacArthur 1955, Loreau et al. 2002, Worm and Duffy 2003, but see May 1972, Pimm 1984, Allesina and Tang 2012). Additionally, increased species diversity may lead to increased resistance and resilience to perturbations such as flooding and drought (Loreau et al. 2002, Matono et al. 2012). Increased community stability and system resistance and resilience will reduce fluctuations in prey populations for semi-aquatic carnivores and potentially affect predator occupancy.

Riparian habitats are often linear and may represent the only suitable habitat for semi-aquatic mammals in the landscape matrix, thereby increasing interactions among the species that utilize them (Bonesi and Macdonald 2004, Ahlers et al. 2010a). These increased interactions may be more important than prey availability in determining predator occupancy. According to the ‘tightrope hypothesis’, removal of riparian buffers for agriculture further reduces available habitat for semi-aquatic mammals and may intensify interactions between and within these populations (Barreto et al. 1998). Therefore, direct interactions among semi-aquatic mammals, including competition, commensalism, and predation, may have strong effects in structuring their occupancy patterns.

North American river otter Lontra canadensis and mink Neovison vison are semi-aquatic carnivores using riparian habitats and, due to overlapping habitat and prey use, competition may occur between these species. River otter are a mid-sized (8–10 kg) carnivore, yet they fill the apex predator niche in riparian-stream systems. In the absence of otter, mink (0.4–1 kg) can assume the role of apex predator in riparian-stream systems. The extent of top–down control exerted by mink is unclear (Roemer et al. 2009); however, they remain an important predator in riparian-stream systems, which are more sensitive to loss of predators than strictly terrestrial or aquatic systems (Soule 2010). Mink and river otter coexist within their native ranges, but niche separation likely occurs through resource partitioning (Melquist et al. 1981, Ben-David et al. 1996). Beavers Castor canadensis modify streams, creating preferred habitat for river otter and mink (Melquist and Hornocker 1983, Dubuc et al. 1990, Baker and Hill 2003, LeBlanc et al. 2007). Although river otter and mink may sometimes prey upon beaver, they do not appear to affect beaver abundance or occupancy; thus, a commensal relationship may exist between beaver and the two predator species (Tumlison et al. 1982, Baker and Hill 2003). River otter will opportunistically depredate muskrat Ondatra zibethicus (Reid et al. 1994, Roberts et al. 2008), especially where muskrat are abundant (Melquist et al. 1981, Melquist and Hornocker 1983). Mink are a primary predator of muskrat, and in some areas the two species have highly synchronized population cycles (Errington 1943, Holmengen et al. 2009, Ahlers et al. 2010b).

The goal of this study was to identify stream and riparian community variables that correlate with the presence of river otter and mink, including the presence of other semi-aquatic mammals. We used multi-season occupancy modelling (MacKenzie et al. 2002, 2003) to address this goal. We have used the general term occupancy to describe the persistent use of an area by river otter or mink, accounting for the probabilities of initial occupancy, colonization (i.e. beginning to use an area that was not used previously), and extinction (i.e. no longer using a previously used area) in a multi-season occupancy model. Our working hypothesis was that apex predators in the system (river otter and mink) are more likely to be
found in sites with high stream quality. We generated several compatible predictions from this hypothesis and compared the relative strength of support for them. We predicted that predator occupancy was positively related to prey availability as measured by fish biomass and abundance. Additionally, we predicted increased diversity of the stream faunal community or the presence of beaver would be positively related to otter and mink occupancy. Finally, we predicted that river otter occupancy would not be affected by mink presence, but mink occupancy would be negatively affected by river otter presence; and that the presence of muskrat would positively affect mink occupancy due to the predator–prey relationship between these two species.

Material and methods

Study area

The study area (44,526 km²; Fig. 1) consisted of watersheds in the southern third of Illinois: Embarras, Little Wabash, Lower Wabash, Skillet, Saline, Cache, Big Muddy, Lower Kaskaskia, Middle Kaskaskia, Shoal, Mississippi and Ohio. Elevation within the study area ranged from 88 to 324 m and the drainage density for the study area was 1.37 km of stream per km². Land-cover for the study area comprised primarily crops (48%), forest (23%), and pasture (15%); followed by areas with minor development (9%) and less than 2% each of open water, woody wetlands, grasslands, high urbanized area, emergent wetlands and bare land (Homer et al. 2015). Mean annual precipitation is 1100 mm with average annual low and high temperatures of 7.1°C and 19.7°C, respectively (<www.usclimatedata.com>).

River otter were listed as state-endangered in Illinois in 1989, and a recovery team was formed in 1993 to plan and implement a reintroduction program (Bluett et al. 1999). Public reports of river otter sightings within Illinois identified relict populations in northwestern Illinois and in the Cache River system of extreme southern Illinois (Fig. 1; Anderson 1995). In an effort to re-establish river otter populations throughout the state, the recovery team released 346 river otter obtained from Louisiana from 1994 to 1996 in central Illinois (Fig. 1; Bluett et al. 1999). Observations of river otter and the presence of kits increased in the release watersheds within a few years (Bluett et al. 1999). Continued surveys indicated that the river otter population had become established throughout most of the state, and the species was delisted by the Illinois Dept of Natural Resources (IDNR) in 2004 (Bluett et al. 2004). A harvest season for river otter opened in November 2012 with a limit of five per person per season. Mink occur throughout Illinois with secure population trends and high rates of detection (Bluett et al. 2006). Mink can be harvested from November to mid-February with no limit.

Site selection

We coordinated data from 77 bridge sites located throughout the study area with streams ranging in size from 2nd to 6th order waterways (Fig. 1; Strahler 1957). Selected sites were basin survey sites (BSS; Bertrand et al. 1996) sampled by IDNR and Illinois Environmental Protection Agency (IEPA) to ensure the use of stream community metrics as covariates in our analysis. As selected by the state, most BSS had historical data on water quality, macroinvertebrate communities, or fisheries. Basin survey sites were selected using random sampling stratified on characteristics of stream habitat, location relative to tributaries, point source pollution, and position within the watershed. We selected BSS that were most recently surveyed by the state (2005–2013) and had data available for fish and macroinvertebrates, as well as data from a survey specifically for mussels. To reduce variation due to sampling, all fish samples were collected using an electric seine. Four sites were completely located on public property and 73 sites were partially or completely located on private property.

Sites were categorized as full sites or half sites. A full site was an 800-m stream segment centred at the bridge or road/stream crossing. A half site was a 400-m stream segment extending either up- or downstream of the bridge. Bridge
sites can have similar detection probabilities to random sites when surveys are of adequate distance (600 m of stream bank; Gallant et al. 2008, Jeffress et al. 2011a). Studies surveying shorter distances have found differences in detection probabilities at bridge and random sites (Crimmins et al. 2009, Just et al. 2012). Probability of detection increases as survey length increases; however, it was necessary to balance effort per site with the number of sites surveyed. We surveyed a 400-m stream reach (800 m of stream bank) because it was the shortest survey length at which the probability of detection of river otter during a single observation was > 0.3 (Gallant et al. 2008, Jeffress et al. 2011a) and greater than the minimum distance needed for detection probabilities at bridge sites to be similar to random sites (Gallant et al. 2008). Estimates of occupancy are relatively unbiased when probability of detection ≥ 0.3 and observations are repeated ≥ 5 times (MacKenzie et al. 2002).

**Sampling design and data collection**

Occupancy models require repeated surveys for species presence so detection probabilities can be estimated (MacKenzie et al. 2002) and occupancy dynamics can be analysed by estimating probability of local site colonization and extinction (MacKenzie et al. 2003). During 2012–2014, a team of two visited each site four times annually: twice (two weeks apart) during winter (January–February) and twice again (two weeks apart) during spring (March–April). Surveys from each member of the team counted as an independent observation, so each site was observed eight times each year. The time between the second and third visit varied between sites, as sites were not sampled in the same order during spring as in winter. This sampling scheme was designed to assess whether detection probabilities for river otter and mink differed between winter and spring.

Multi-season occupancy models require primary and secondary sampling periods, which allows for the calculation of probability of colonization and extinction during the intervals between primary sampling periods (MacKenzie et al. 2003). Our design included two primary periods (winter and spring) per year for three study years, totalling six primary sampling occasions (two observers during two visits, described here as ‘observations’) per primary period. A major assumption of multi-season occupancy modelling is that occupancy is constant within a primary sampling period (MacKenzie et al. 2006). By dividing each year into two primary periods, we could meet this assumption, as river otter and mink are more mobile during spring than winter (Lariivière 2003, Melquist et al. 2003). Logistical and land-owner permission issues resulted in only 62 of the 77 sites being sampled in all six periods. The other 15 sites were sampled in four periods. All 77 sites were used in the analyses.

The experimental unit was a 400-m stream segment, with a total of 800 m of stream bank surveyed by each observer. At a full site, one observer surveyed 400 m of stream upstream of the bridge, while the other observer surveyed 400 m of stream downstream of the bridge. Both observers independently surveyed the same 400 m of stream when surveying a half site. Surveys consisted of the observer walking along the stream bank looking for signs (tracks, scat or evidence of foraging) of mammals (Crimmins et al. 2009, Jeffress et al. 2011a, Lesmeister and Nielsen 2011). Observers recorded all fresh mammal signs found, including sign type and species, and a visual estimation of % substrate available (to nearest 10%) for track imprints. Substrate comprised % of sand, mud, or other soft bank surfaces. Surveys were conducted by kayak or canoe when streams were too deep to wade. Survey-based detection covariates included characteristics of the site, survey unit, observer, and how the survey was conducted (i.e. kayak/canoe versus walked segment; Table 1).

We obtained temperature (average, maximum and minimum) and precipitation (total and maximum one-day precipitation) data for the two-week period before each site visit from 38 local airport weather stations (www.wunderground.com>). To address spatial mismatch between sampling sites and climatic data collection, weather data were spatially interpolated to estimate values at each stream site. Interpolation was conducted in ArcMap 10.2.1 (ESRI 2011) using the spline tool for temperature variables and inverse-distance weighting for rainfall (Dirks et al. 1998, Childs 2004, Chen and Liu 2012). Temperature range during the two-week period was then calculated from the interpolated maximum and minimum temperatures for each site.

Our hypothesis assumed that the presence of river otter and mink is affected by stream quality, with specific predictions regarding prey availability and community diversity. Therefore, we developed a series of prey covariates based on otter and mink foraging behaviour. Otter (e.g. North American, European *Lutra lutra*) primarily forage based on prey availability (Erlinge 1968, Anderson and Woolf 1987, Lanszki and Körmendi 1996), and mink are most active in areas where prey abundance and availability are high (Burgess and Bider 1980, Wise et al. 1981, Lariviè re 2003, Wolff et al. 2015). River otter primarily prey on fish (Roberts et al. 2008, Barding and Lacki 2012, Feltrop et al. 2016), but also consume crustaceans and molluscs (Satterthwaite-Phillips et al. 2014, Freteug et al. 2015, Feltrop et al. 2016). Diets of mink and river otter overlap, however, mink are a generalist carnivore taking more terrestrial prey than river otter (Wise et al. 1981).

Accordingly, our prey covariates included metrics of fish and mussel communities. Unfortunately, data on crayfish communities were not available. We calculated fish species richness, biodiversity, abundance and biomass from data collected by IDNR during their most recent survey of BSS (2005–2013). Data on sampling method, species, number and total length of fish collected during each survey were obtained from the state fish database maintained by the Illinois Natural History Survey (INHS; J. A. Stein, Illinois Natural History Survey, pers. comm.). Species diversity was calculated using the Shannon–Weaver index and biomass was calculated using length–weight relationships (Quist et al. 1998, Schneider et al. 2000). When species-specific equations
for length–weight relationships were not available or in the case of hybrids, equations for species of similar body type or the first species listed in the hybrid description were used.

Fish species richness was simply the number of species found during the survey and fish abundance was the total number of individual fish collected. Centrarchidae, Catostomidae, Cyprinidae and Ictaluridae have been reported as the most important families consumed by otter, varying in importance based on location (Roberts et al. 2008, Stearns and Serfass 2011, Barding and Lacki 2012). Species within these families were considered preferred fish species for our analyses.

Additional stream diversity metrics include the macroinvertebrate community. Data from a general macroinvertebrate survey was obtained from IEPA (T. J. Reuter, Illinois Environmental Protection Agency, pers. comm.). The macroinvertebrate index of biotic integrity (IBI) was calculated by the IEPA from measurements related to the macroinvertebrate assemblage (IEPA 2011). There is no standard method to calculate a macroinvertebrate IBI; however, as calculated by the IEPA, it combines multiple aspects of the macroinvertebrate assemblage (e.g. richness, intolerant taxa, indicator taxa) to assess impacts of disturbance across the community (Rosenberg and Resh 1993, IEPA 2011). Finally, the INHS surveyed sites throughout the state for mussels. We obtained data regarding mussel species richness and mussel community index (MCI), based on species richness, abundance, reproduction, and intolerance, from technical reports (Shasteen et al. 2011, 2012a, b, c, d, e, 2013).

Our use of large data sets collected by multiple groups for other purposes imposed limitations and assumptions. We assumed these data sets were representative of the stream community at the time of river otter and mink surveys, although most fish, macroinvertebrate, and mussel data were collected before our sign surveys in 2012–2014. Fish were primarily sampled from 2007 to 2012; however, we also used two samples from 2005 and one sample from 2013.
We assumed that the fish collected in the sample were equally representative of the stream population at every site and that there was limited bias to the type and number of fish sampled. Macroinvertebrates were primarily sampled from 2007 to 2011, but we also used two samples from 2005. Mussels were sampled from 2009 to 2012.

River otter and mink are likely to interact with each other as well as with other semi-aquatic mammals, primarily beaver and muskrat, in the riparian-stream system (Melquist et al. 1981, Melquist and Hornocker 1983, Ben-David et al. 1996). We tested for relationships between river otter and mink occupancy with each of the other semi-aquatic mammals. Probability of detection within a primary period (P) was ≥ 0.95 for all four species, based on per observation probability of detection for each species (p) and the number of observations per period (v):

\[ P = 1 - (1 - p)^v \]

Therefore, we did not account for detection probability when including the presence of other mammal species as predictors when modelling the probability of colonization or extinction of river otter and mink. We incorporated two management covariates into multi-season occupancy models of river otter: a variable indicating whether a site was located in a watershed where river otter were reintroduced or where a remnant population was believed to exist (Anderson 1995, Bluett et al. 1999), and the distance from the survey site to the nearest point where river otter were reintroduced (Bluett et al. 1999).

**Data analyses**

Multi-season occupancy models were run in program R (<www.r-project.org>) using package ‘unmarked’ (Fiske and Chandler 2011). Multi-season occupancy models have four base parameters (detection, initial occupancy, colonization, and extinction) that were estimated using a hierarchical method (Fig. 2a; Cosentino et al. 2010, Ahlers et al. 2016) with variables available for each respective parameter (Table 1). We first determined the top model for probability of detection (p) while holding the other three parameters constant. Then we used the top detection model to find the top initial occupancy (Ψ) model while holding colonization (γ) and extinction (ε) constant. We used the combined top detection and initial occupancy model to determine the top colonization model while holding the final parameter constant. Finally, we used the top combined detection, initial occupancy, and colonization model to determine the top model for probability of extinction. The top model at each step was determined using Akaike’s information criterion (AIC; Burnham and Anderson 2002). Models were created using a decision tree (Fig. 2b) with a ΔAIC<4 informative model restriction (Burnham et al. 2011; additional information regarding the modelling process is available in Supplementary material Appendix 1). Variables were not combined into a single model if variables were correlated \((r \geq 0.7)\) as tested using a Pearson correlation test or if they were both in the time, management, or mammals variable classes (Table 1). This process was repeated for each species. Variables in the time class were not assessed for probability of colonization and extinction of mink due to the high probability of detection and persistence of this species within the study area (Bluett et al. 2006). Due to the complexity of the hierarchical analysis, beta values and standard errors change throughout the modeling process. The values reported in the results are from the final model of multi-season occupancy for each species. We assessed model fit of the top overall model for each species using a parametric bootstrap with 1000 replicates and the \(\chi^2\)-statistic (Fiske and Chandler 2011, Kéry and Chandler 2012).

**Data deposition**

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.2mv5722> (Holland et al. 2018).

**Results**

**River otter**

River otter were detected at least once at 63 of 77 (81.8%) sites throughout the study. Percent of sites with detections increased slightly from 2012 (56.5%) to 2013 (58.4%) and 2014 (67.5%). River otter tracks were the primary sign available in 91% (407 of 445 detections) of all river otter detections. Latrines were found during 19% (83 of 445 detections) of river otter detections, but tracks also were found by the same observer for 55% (46 of 83) of latrine detections. The final model had adequate model fit \((p = 0.89)\).

Nine univariate models of detection probability ranked above the null model, with the top univariate model including % substrate availability (Supplementary material Appendix 2 Table A1). No variables were combined because the second-best model had a ΔAIC value of 25.38. The top model for probability of detection included a positive relationship for % substrate availability \((\beta = 0.25, SE = 0.04); Table 2\). Only one model of initial occupancy had a ΔAIC lower than the null model (Supplementary material Appendix 2 Table A2). This top model indicated that initial occupancy of river otter in 2012 was negatively related to distance from the surveyed site to the nearest otter reintroduction point \((\beta = -0.02, SE = 0.01); Fig. 3\).

Two temporal univariate models (beaver and mink presence) had lower ΔAIC values than the null colonization model. The variable from the top temporal model, beaver presence, was used in combination with all non-temporal colonization variables (those not in the time or mammals variable classes; Table 1). Six of these two combination variable models ranked higher than the beaver-only model for probability of colonization, but only the top two (macroinvertebrate IBI, followed by fish richness) had a ΔAIC ≤ 4 (Supplementary material Appendix 2 Table A3). The top model for probability
The top model for probability of extinction therefore included variation by survey period and preferred fish richness (Table 2). Probability of extinction varied by survey period (spring 2012–winter 2013: $\beta = 0.64$, $SE = 0.64$; winter 2013–spring 2013: $\beta = -0.76$, $SE = 0.77$; spring 2013–winter 2014: $\beta = 0.23$, $SE = 0.63$; winter 2014–spring 2014: $\beta = -2.78$, $SE = 1.41$) and preferred-fish species richness ($\beta = -0.07$, $SE = 0.04$). We transformed probability of extinction into the probability of persistence ($1 - \varepsilon$), or the probability that a site would remain occupied (Fig. 5). Persistent use of sites by river otter increased throughout the study with higher persistence during short intervals. The inclusion of survey period in the final model was primarily driven by the high persistence of river otter during the winter to spring 2014 interval. River otter were more likely to persist in sites with increased preferred-fish species richness.
Mink were detected at least once at 76 of 77 (98.7%) sites throughout the study. Percent of sites with detections remained consistently high throughout the study period: 2012 (100.0%), 2013 (93.5%), and 2014 (93.5%). Tracks were the primary evidence of mink presence (99% of all mink detections). The final model had adequate model fit ($p = 0.99$).

Twelve univariate models of detection probability ranked above the null model (Supplementary material Appendix 3 Table A5). No variables were combined because the second-best model had a ΔAIC value of 8.78. The top model for probability of detection included variation due to survey period (spring 2012: $\beta = 0.67$, SE = 0.23; fall 2013: $\beta = 0.81$, SE = 0.22; spring 2013: $\beta = 0.78$, SE = 0.21; fall 2014: $\beta = 0.24$, SE = 0.21; spring 2014: $\beta = 0.29$, SE = 0.22; Table 3).

No univariate models ranked higher than the null model for probability of initial occupancy, so the top detection model and null model for initial occupancy were used in modelling the probabilities of colonization and extinction of mink (Supplementary material Appendix 3 Table A6). All temporal univariate models (muskrat, otter, and beaver presence) had lower ΔAIC values than the null colonization model. The variable from the top temporal model, muskrat presence, was used in combination with all non-temporal colonization variables. Four of these
two-variable combination models for probability of colonization (all $\Delta$AIC $\leq$ 4) ranked higher than the muskrat presence model, with fish species richness ranking in the top model (Supplementary material Appendix 3 Table A7). One of these four models (non-native fish species richness) did not converge properly, so this variable was not used in combination models. Additional variable combinations did not improve the top combined model for probability of colonization (Table 3). Probability of colonization by mink increased with increased fish species richness ($\beta = 0.12$, SE = 0.07) and when muskrat were present ($\beta = 1.62$, SE = 0.92; Fig. 6).

No temporal variable model ranked above the null probability of extinction model for mink, so all non-temporal variables were run as univariate models. Of these, two univariate models ranked above the null model for probability of extinction (Supplementary material Appendix 3 Table A8). Both predictors were related to the mussel community and not combined due to correlation ($r = 0.86$, $p < 0.01$). The top model indicated that the probability of extinction decreased with increasing mussel community index ($\beta = -0.09$, SE = 0.05).

**Discussion**

Measurements of faunal diversity at multiple trophic levels in the riparian-stream community were positively related to occupancy of river otter and mink as predicted. Presence of these riparian predators was not only related to increased prey diversity, but also to increased diversity at lower trophic levels, indicating a link between predator presence and riparian-stream system quality. Most studies of river otter and mink occupancy have not used aspects of prey diversity or availability as covariates (Jeffress et al. 2011b, Williamson and Clark 2011, Schooley et al. 2012); however, Wolff et al. (2015) found a positive effect of crayfish abundance on mink occupancy. The prominence of metrics of species diversity in our top models may be due to temporal mismatch between when stream community and mammal community data were collected. Aspects of species diversity are less likely to fluctuate seasonally and over time than abundance or biomass (Dahlberg and Odum 1970). Also, we had no evidence of major changes to our sites in the time between when the two types of data were collected. Additionally, due to the yearly variation of when fish and macroinvertebrate data were collected and the large scale of the study, we do not believe that any one disturbance event would affect our results.

**Table 3.** Top five competitive ($\Delta$AIC $\leq$ 4) model results for probability of detection ($p$), initial occupancy (Ψ), colonization ($\gamma$), and extinction ($e$) of mink in southern Illinois, 2012–2014. Models are ranked based on the lowest Akaic’s information criterion (AICc) where $\Delta$AIC = AICc − minimum AIC, $K =$ number of parameters, and $w = $ model AIC weight, and LL = log likelihood. Variables are defined in Table 1. Additional models can be found in Supplementary material Appendix 3 Table A5–A8.

| Parameter              | Model                                                                 | $\Delta$AIC | K   | w     | LL         |
|------------------------|-----------------------------------------------------------------------|--------------|-----|-------|------------|
| Detection              | $\Psi(\cdot) \gamma(\cdot) e(\cdot) p(\text{survey period})$        | 0.00         | 9   | 0.99  | -1008.35   |
| Initial occupancy      | $\Psi(\cdot) \gamma(\cdot) e(\cdot) p(\text{survey period})$        | 0.00         | 9   | 0.31  | -1008.35   |
|                        | $\Psi(\text{total fish sp. richness}) \gamma(\cdot) e(\cdot) p(\text{survey period})$ | 1.12         | 10  | 0.18  | -1007.91   |
|                        | $\Psi(\text{fish species diversity}) \gamma(\cdot) e(\cdot) p(\text{survey period})$ | 1.67         | 10  | 0.14  | -1008.18   |
|                        | $\Psi(\text{mussel richness}) \gamma(\cdot) e(\cdot) p(\text{survey period})$ | 1.70         | 10  | 0.13  | -1008.20   |
|                        | $\Psi(\text{mussel community index}) \gamma(\cdot) e(\cdot) p(\text{survey period})$ | 1.85         | 10  | 0.12  | -1008.27   |
| Colonization           | $\Psi(\cdot) \gamma(\text{muskrat + total fish sp. richness}) e(\cdot) p(\text{survey period})$ | 0.00         | 11  | 0.21  | -1003.46   |
|                        | $\Psi(\cdot) \gamma(\text{muskrat + total fish sp. richness + mussel richness}) e(\cdot) p(\text{survey period})$ | 0.15         | 12  | 0.19  | -1002.54   |
|                        | $\Psi(\cdot) \gamma(\text{muskrat + non-native fish sp. richness}) e(\cdot) p(\text{survey period})$ | 0.66         | 11  | 0.15  | -1003.79   |
|                        | $\Psi(\cdot) \gamma(\text{muskrat + mussel richness}) e(\cdot) p(\text{survey period})$ | 0.91         | 11  | 0.13  | -1003.92   |
|                        | $\Psi(\cdot) \gamma(\text{muskrat + total fish diversity}) e(\cdot) p(\text{survey period})$ | 1.17         | 11  | 0.12  | -1004.05   |
| Extinction             | $\Psi(\cdot) \gamma(\text{muskrat + total fish sp. richness}) e(\text{mussel community index}) p(\text{survey period})$ | 0.00         | 12  | 0.29  | -1001.64   |
|                        | $\Psi(\cdot) \gamma(\text{muskrat + total fish sp. richness}) e(\text{mussel species richness}) p(\text{survey period})$ | 0.88         | 12  | 0.19  | -1002.08   |
|                        | $\Psi(\cdot) \gamma(\text{muskrat + total fish sp. richness}) e(\cdot) p(\text{survey period})$ | 1.64         | 11  | 0.13  | -1003.46   |
|                        | $\Psi(\cdot) \gamma(\text{muskrat + total fish sp. richness}) e(\text{beaver presence}) p(\text{survey period})$ | 2.11         | 12  | 0.10  | -1002.70   |
|                        | $\Psi(\cdot) \gamma(\text{muskrat + total fish sp. richness}) e(\text{total fish sp. diversity}) p(\text{survey period})$ | 2.31         | 12  | 0.09  | -1002.80   |

**Figure 5.** Modelled relationship of preferred fish species richness to the probability of persistence between all survey periods for river otter in Illinois, 2012–2014, using parameter estimates from final model.
Otter occupancy dynamics

Our results show correlations between river otters and stream faunal communities. They supported our predictions of positive relationships between river otter and diversity at multiple trophic levels. Macroinvertebrate IBI was the most important (as determined by ratio of SE to $|\beta| < 0.5$) variable affecting site colonization by river otter. As calculated by the IEPA, this IBI combines multiple aspects of the macroinvertebrate assemblage (e.g., richness, intolerant taxa, indicator taxa) to assess impacts of disturbance across the community (Rosenberg and Resh 1993, IEPA 2011), with higher IBI levels indicative of a diverse community intolerant of human disturbance. Although our analyses were unable to determine if the relationship between river otter use and macroinvertebrate communities at stream sites was due to bottom–up or top–down effects, the correlation was clear. Relationships between macroinvertebrate and fish communities can be tenuous and are often scale-dependent, with both abiotic and biotic factors affecting each community (Cooper et al. 1998, Kilgour and Barton 1999, Heino et al. 2005), but this does not rule our potential top–down effects of river otter site use. Conversely, because macroinvertebrate IBI is used as a biological indicator of stream quality (Rosenberg and Resh 1993), the relationship to river otter site use may simply be an indication that river otters demonstrate a bottom–up response to higher-quality streams.

River otter colonization and persistence was related to total and preferred fish species richness, respectively, providing additional support for our overall hypothesis. Although these variables were considered less important than macroinvertebrate IBI (SE: $|\beta| > 0.5$), their presence in the top models for two aspects of multi-season occupancy modelling and a cumulative weight of 0.38 (Table 2) for models containing preferred fish richness and overall fish richness for probability of extinction indicates a relationship between river otter occupancy and fish species richness. This relationship may be due to top–down effects as expected by blocking competitive exclusion or mesopredator release within the fish community (Estes et al. 2011). Alternatively, river otter may be responding to higher stream quality or system stability. Fish species richness is positively related to stream habitat heterogeneity (Gorman and Karr 1978, Guégan et al. 1998). Diverse fish communities also can lead to increased resistance and resilience in quality streams (Matono et al. 2012). Regional diversity can enhance resistance and resilience to perturbations, helping to maintain ecosystem integrity (Loreau et al. 2002).

Preferred and overall fish abundance or biomass did not feature in competitive models for initial occupancy, colonization or persistence. Therefore, we did not find support for the prediction that river otter presence is driven by prey availability. River otter primarily eat fish and crayfish based on availability (Roberts et al. 2008, Stearns and Serfass 2011, Fretueg et al. 2015), but data for crayfish abundance and biomass were not available for our study sites and thus not used in this analysis. We did not use any interactions or quadratic terms in our analysis. It is possible that these types of non-linear relationships may have been better suited for fish abundance and biomass, because there may be a threshold maximum fish abundance or biomass that an individual river otter can consume. Seasonal variation in abundance and biomass, and temporal mismatch between years sampled for fish and years surveyed for river otter also may explain why fish biomass and abundance were poor predictors of otter occupancy. Additionally, fish biomass may have been a poor predictor of otter occupancy because high biomass could be due to larger fish in the stream system. River otter consume some fish size classes more often than others (Erlinge 1968, Lanszki et al. 2001, Lanszki and Sallai 2006, Stearns and Serfass 2011). Thus, fish biomass as calculated in this study may not be a good indicator of biomass of fish available to river otter, especially in sites with fish larger than 20 cm and 1000 g.

Beaver presence was in the top model for probability of river otter colonization providing some support for our prediction that river otter occupancy would be higher in areas where beaver were present. High SE (SE: $|\beta| > 0.5$) indicates that this relationship may not be as strong as indicated by previous studies. River otter are more likely to use sites where beaver have been active for prolonged periods (LeBlanc et al. 2007), suggesting that river otter use sites that are most affected by beaver behaviour, such as dam building. Beaver dams alter both physical and ecological aspects of the stream. They can increase water clarity, which aids in the ability of river otter to capture prey. Dams also lead to increased fish biomass and diversity and numbers of macroinvertebrates (McDowell and Naiman 1986, Alexander 1998, Colleen and Gibson 2000). The strength of beaver effects on river otter colonization may be more influenced by the changes in the stream community induced by beaver to the stream system, such as increased fish richness, rather than physical presence. Areas of high beaver density within the study area (Bloomquist and Nielsen 2010), high occupancy of beaver throughout the
study (Holland 2016), and lack of beaver dams within surveyed segments, may have muted the relationship between river otter occupancy dynamics and beaver presence.

Our results suggested that river otter are still expanding their range, which is supported by other recent studies (Nielsen 2016). Previous studies have primarily used habitat variables and physical stream characteristics to predict probability of occupancy of river otter (Jeffress et al. 2011b, Bennett 2014, Holland 2016). In contrast, we showed that aspects of population expansion and community diversity are suitable predictors of river otter occupancy, especially in areas where reintroduction has occurred. Range expansion by recolonizing populations has been described as a piecewise linear relationship, where expanding populations stall in high-quality habitats and move through low-quality habitat (Lubina and Levin 1988). The strength of the relationship between distance from otter reintroduction point and probability of initial occupancy may be affected by the remnant population (Fig. 1, Anderson 1995), as the presence of the remnant population in the present work reduced the strength of the relationship in comparison to other studies (Williamson and Clark 2011).

Temporal (period, season, year) variables can be important predictors of the probability of colonization or extinction when using multi-season occupancy models (MacKenzie et al. 2003, Dugger et al. 2011, van der Merwe et al. 2016). Overall, the probability of river otter persistence during within-year and between-year intervals increased over the two-year study period (Fig. 5). These increases provide additional support that the river otter population in the study area is becoming more established. It is also important to note that part of the seasonal variation was due to differences in the interval length. Within-year intervals (range in days: 13–80, average 41.4, median 41) had a higher probability of persistence (i.e. lower extinction probability) than between-year intervals (range in days: 258–338, average 297.2, median 297). This effect is likely due to the shorter interval, but also may be due to the overlap between river otter breeding and parturition behaviour with the spring survey period each year (Melquist et al. 2003). During March and April, female river otter remain in areas near their birthing and rearing den site (Melquist and Hornocker 1983), whereas male river otter are increasing movement for the breeding season. Increased movements by males may result in higher site use and increased probability of persistence from winter to spring survey periods.

River otter presence was primarily identified by tracks rather than any other sign type, so the importance of % substrate availability in detection is intuitive. Other studies of river otter occupancy have found effects of substrate type on probability of detection, with mud and sand having the highest probabilities of detection followed by litter and snow (Jeffress et al. 2011b, Williamson and Clark 2011, Bennett 2014). Additional variables affecting river otter detection in other studies included month, water depth, and observer (Williamson and Clark 2011, Bennett 2014).

Mink occupancy dynamics

Our overall hypothesis that occupancy of mink was related to stream quality was supported, albeit weakly, because consistent high site use by mink throughout the study resulted in multiple competitive models. These results made it difficult to discern which variables were most important to mink occupancy. Variables in the top model for probability of colonization and extinction had SE:β of ~ 0.56. Mink appeared to colonize stream sites based on increased presence of larger prey items such as muskrat, but persistence at the site was better predicted by the mussel community. The correlation between muskrat presence and mink colonization is most likely due to a combination of the predator–prey relationship between the species (Errington 1943, Ahlers et al. 2010b) and the similar effects of flooding and drought on these small semi-aquatic mammals (Ahlers et al. 2015). Other studies have found a relationship between mink occupancy and muskrat presence (Ahlers et al. 2016).

Increased fish species richness appeared to increase probability of colonization by mink, similarly to river otter. The linkage between fish species richness and stream quality with mink is likely similar to the parallel relationship for river otter. Aspects of the mussel community positively affected both probability of colonization (second best model; Table 3) and persistence, indicating the importance of this aspect of the stream community to occupancy by mink. Mussels may benefit mink by increasing stream clarity (Vaughn and Hakenkamp 2001) and as a potential food source (Pennak 1989). In addition to these direct benefits, mussels require good stream quality and appropriate host fish populations and therefore may be indicators of stream health (Williams et al. 1993).

We did not find support for our prediction that mink would be negatively affected by river otter presence due to competition between the species. Mink presence was a positive predictor of river otter occurrence in another occupancy study (Bennett 2014); however, mink presence may have been an indirect measurement of prey availability because both species are likely to occur in areas with high prey resources (Larivière 2003, Melquist et al. 2003). Resource partitioning can occur between North American river otter and mink in freshwater environments, with low prey availability leading to competition (Melquist et al. 1981). The logical extension is that competition will not occur in habitats with high prey availability, which may have driven the results that we observed. The relationship between these two species should be re-evaluated over time as river otter populations increase state-wide.

Probability of detection for mink varied by period and was highest during spring 2012 and 2014. Other studies in Illinois have indicated that mink have a high probability of detection that varies temporally (Bluett et al. 2006, Schooley et al. 2012, Ahlers et al. 2015). Observer, rain, and substrate are other variables affecting probability of detection for mink in Illinois (Schooley et al. 2012, Ahlers et al. 2015), but were not in the top model for probability of detection.
in this study (but see Holland 2016). High site use by mink during the first survey period resulted in no tested variables affecting probability of initial occupancy.

Summary

It has been suggested that apex predators such as river otter and mink may increase biodiversity within a system (Estes et al. 2011). We found positive associations of indices of biodiversity such as macroinvertebrate IBI, fish species richness, and mussel richness with occupancy by river otter and mink. However, our study was not designed to determine the direction of causal links between species occurrence and indices of the stream community. For example, do river otter affect fish species richness or do high numbers of fish species increase site attractiveness to otter? If river otter and mink have continued to use the same sites for many years, even if not consistently, do they contribute to increases or decreases in fish richness? Understanding the direction of this relationship can only be accomplished with design and analysis that permits the exploration of causal hypotheses, such as structural equation modelling or long-term manipulative experiments.

If this relationship is due to site attractiveness or quality, it may suggest that habitat heterogeneity and system stability are important to river otter and mink site use. Local habitat heterogeneity is positively linked to community species richness (Gorman and Karr 1978, Rosenzweig 1995, Kerr and Packer 1997, Guégan et al. 1998), and thus richness in the riparian system is likely to increase with habitat complexity. Increased species diversity also can increase the number of food web linkages, which in turn increases community stability (MacArthur 1955, Loreau et al. 2002, Worm and Duffy 2003, but see May 1972, Pimm 1984, Allesina and Tang 2012). Understanding the direction of the relationship between semi-aquatic carnivores and stream diversity is necessary to elucidate the role of habitat heterogeneity and system stability as drivers of that relationship.

The European otter has been described as a bioindicator due to their range overlap with intolerant macroinvertebrate groups (Lunnon and Reynolds 1991, Ruiz-Olmo et al. 1998); conversely, wide distributions and generalist preferences (e.g., diet, habitat) have been touted as reasons why European river otter are poor bioindicators (Reid et al. 2013). During our study, river otter were still expanding their range in the study region, thus the relationship between occupancy by river otter and stream quality cannot be used to support the concept that river otter are bioindicators. Expanding populations at low densities may colonize and persist in optimal habitat while suboptimal habitat is passed by when encountered (Lubina and Levin 1988). The high occupancy of mink during this study gives weak support to any relationship between habitat quality and mink presence; density or abundance data would be needed to better understand this relationship. Additionally, our results do not reflect how sites are used; it was not possible to determine if an area was used for foraging, breeding, or strictly as a travel corridor.

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Supplementary material (available online as Appendix oik-05085 at <www.oikosjournal.org/appendix/oik-5085>). Appendix 1–3.