

# Common reed (*Phragmites australis*) invasion and amphibian distribution in freshwater wetlands

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**Abstract** Invasive plants can substantially modify wetland structure and animal distribution patterns. In eastern North America, a Eurasian haplotype of the common reed (*Phragmites australis*, haplotype M) is invading wetlands. We studied the invasion of common reed in freshwater wetlands of an urbanized landscape and its effects on the distribution of amphibians at different life stages. Specifically, we hypothesized that the probability of reed invasion would be greatest in wetlands near anthropic disturbances. We predicted that the probability of desiccation at sampling stations increases with reed cover. Furthermore, we expected that wetlands invaded by common reed would have lower amphibian abundances, apparent survival, and rates of recruitment. We conducted trapping surveys to compare anuran assemblages of tadpoles, juveniles, and adults in 50 wetlands during two field seasons. The probability of reed invasion in wetlands increased with the cover of heavily-managed areas within 1,000 m and the distance to the nearest forest, but decreased with the

length of roads within 1,000 m. The probability of station desiccation increased with reed cover. We found no evidence of a negative effect of reed presence on anuran population parameters, at any life stage. Landscape variables, such as the percent cover of forest or heavily-managed areas within a given radius from each wetland, influenced the abundance or the apparent survival of juvenile frogs and the abundance of ranid tadpoles. Our results show that amphibian patterns depend more strongly on the structure of the landscape surrounding wetlands than on exotic reed invasion in wetlands.

**Keywords** Anurans · Demographic parameters · Detectability · Frogs · Landscape structure · Invasive species · Exotic plant

## Introduction

Invasions by exotic species can substantially alter biotic communities and ecosystem functions (Drake et al. 1989; Gurevitch and Padilla 2004; Davis 2009). Wetlands are a case in point, where exotic invasive plants can alter water regimes, the structure, and functions of such ecosystems (Macdonald et al. 1989; Meyerson et al. 1999). Invasive plants monopolize space and nutrients, excluding native flora and fauna (Lockwood et al. 2001; Kercher and Zedler 2004; Zedler and Kercher 2004). Exotic plant invasion can reduce the abundance of fish (Able and Hagan 2000),

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invertebrates (Cheruvilil et al. 2002; Canhoto and Laranjeira 2007), and disturb amphibian larval development and behavior (Maerz et al. 2005a; Watling et al. 2011a; Cotten et al. 2012). Among invasive plants, the common reed (*Phragmites australis*) has been the focus of recent investigations in brackish and freshwater wetlands.

The Eurasian haplotype of common reed (*P. australis*, haplotype M) is one of the most aggressive exotic plants in North America. This large perennial grass occurs in colonies containing up to 325 stems/m<sup>2</sup> (League et al. 2007). The range expansion of common reed is largely associated with anthropogenic activity (Chambers et al. 1999; Saltonstall 2002). The ecological impacts of common reed invasion are varied. Its rapid growth and high organic sediment accumulation rate alter wetland hydrology and ecosystem functions as well as physical and biogeochemical processes (Meyerson et al. 1999; Windham and Lathrop 1999; Rooth et al. 2003). The effect of the common reed on animal communities is less straightforward than on plants. Studies have documented both positive and negative effects of reed establishment on invertebrates, fish, or birds (Benoit and Askins 1999; Talley and Levin 2001; Warren et al. 2001). To date, research on amphibians in the context of reed invasion or other exotic plants has almost exclusively focused on larval development (Maerz et al. 2010; Cohen et al. 2012; Rogalski and Skelly 2012, but see Maerz et al. 2005b and Watling et al. 2011b).

Wetland-breeding amphibians are among the vertebrates most likely to be influenced by reed invasion. First, wetland-breeding amphibians have a biphasic life cycle with important morphological and physiological changes (Wilbur 1980). Second, amphibians maintain a close relationship with aquatic environments and the surrounding terrestrial habitats (Sinsch 1990; Pope et al. 2000). The epidermis of amphibians is permeable and must remain moist to allow gas and water exchanges (Thorson and Svihla 1943; Thorson 1955). Third, landscape composition (i.e., type and quantity of suitable habitat) and landscape configuration (e.g., patch arrangement, habitat fragmentation) influence the connectivity between the different habitats necessary to complete amphibian life cycles (Semlitsch 2002; Mazerolle et al. 2005). Consequently, a reduction in quality of either terrestrial or aquatic habitats can potentially lower amphibian reproductive success and limit successful colonization

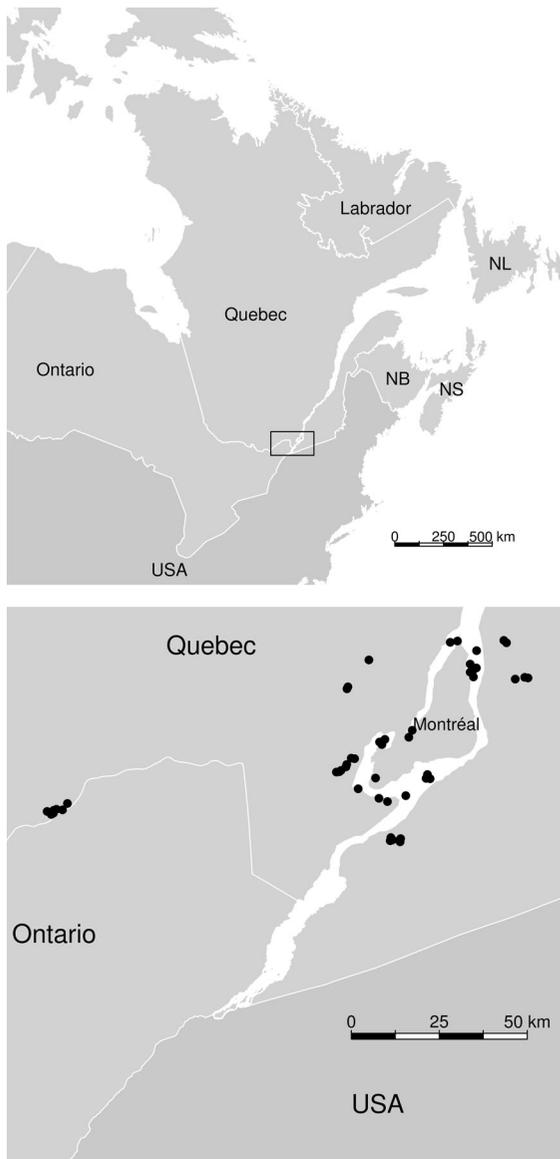
(Semlitsch 2002). Reed invasion entails major changes in wetlands (Meyerson et al. 1999). These changes might also influence amphibian distribution in the landscape.

In this study, we assess the importance of anthropic disturbances on reed invasion in wetlands. We also evaluate the impact of local and landscape characteristics on amphibian abundance dynamics at different life stages, after accounting for detection probability. Here, we define local characteristics as variables at the wetland scale such as wetland size or presence of common reed. Landscape characteristics relate to either landscape composition (e.g., cover of certain habitat within a given radius) or landscape configuration (e.g., distance to a given habitat). In these assessments, we contrasted forest patches against areas undergoing heavily-managed land uses such as residential areas, parking lots, roads, and agriculture. We hypothesized that (a) reed invasion increases with heavily-managed areas, (b) an increase in reed cover decreases habitat quality by increasing desiccation rate, (c) amphibian habitat use is negatively influenced by reed invasion with the strongest effects on early developmental stages.

## Methods

### Study area

We conducted most of our study within a 50 km radius of the city of Montréal, Québec, Canada, in the mixedwood plains ecozone (Fig. 1). The climate is wet and defined by warm to hot summers and cool winters with an average year temperature of 6.2 °C and total precipitations of 979.1 mm (Environment Canada, <http://climate.weatheroffice.gc.ca/>). We targeted 50 wetlands within our study area, 25 of which were invaded by the exotic *P. australis*. These wetlands consisted of ponds, marshes, swamps, and oxbow ponds. Because relatively undisturbed and uninvaded sites were difficult to find within the parks of the city of Montréal, we also considered seven uninvaded wetlands from the Plaisance National Park (ca. 110 km away) to reach our goal. With these constraints, we selected wetlands randomly within our study area. Wetlands ranged in area between 0.08 and 3 ha, and were separated by a minimum of 500 m. We chose this distance to ensure independence among sites as the



**Fig. 1** Wetlands sampled in 2009 and 2010 in the Montréal area, Canada

amphibian species in our study have low dispersal abilities (see “[Species under study](#)” section below). Wetlands were surrounded by different environments, either deciduous forest, agricultural fields, roads, or urbanized lands (e.g., parking lots, residential areas).

#### Species under study

Nine anuran species occur in the study area: northern leopard frog (*Lithobates pipiens*), wood frog

(*Lithobates sylvaticus*), bullfrog (*Lithobates catesbeianus*), green frog (*Lithobates clamitans*), pickerel frog (*Lithobates palustris*), American toad (*Anaxyrus americanus*), gray treefrog (*Hyla versicolor*), spring peeper (*Pseudacris crucifer*), and the western chorus frog (*Pseudacris triseriata*). At our latitude, most of these species breed between April and August (Wright and Wright 1949; Desroches and Rodrigue 2004). The amphibians in our study are semi-aquatic species, and require a terrestrial core area adjacent to the wetland to forage, breed, disperse, or overwinter (Semlitsch 2008). The habitat used by frogs can extend to a mean maximum radius buffer of 368 m around breeding wetlands (Martof 1953; Dole 1965; Semlitsch and Bodie 2003). Studies on some of the above-mentioned species reported migration and dispersal distances rarely exceeding 1 km (Dole 1968; Dole, 1971; Berven and Grudzien 1990; Dodd 1996).

#### Amphibian sampling

Each wetland was sampled at several fixed stations along its perimeter. The number of stations increased with wetland area. We established two sampling stations for the first 25 m<sup>2</sup> and added a station whenever the wetland surface doubled (Adams et al. 1997). Sampling stations were positioned on the wetland perimeter from a random selection in ArcGIS 9.3 (ESRI 2008) with the condition that adjacent stations had to be separated by at least 30 m. For the two smallest sites (<0.27 ha), we prioritized the minimum distance between sampling stations rather than the effort. Based on these rules, we established a total of 455 sampling stations, each wetland having between 4 and 11 sampling stations (average of 9.1 per wetland). We sampled anurans using minnow traps (Adams et al. 1997).

We determined the life stage of all individuals trapped: adult, juvenile, and tadpole. We considered an individual as a juvenile if it had metamorphosed during the field season in which it was captured. We based our classification of juvenile or adult on the known minimal size of the different species in our study area (Desroches and Rodrigue 2004). Traps were set at the call stations described above for two consecutive days. We monitored traps each morning to record and release captured animals. At each trap, we identified adults and juveniles to species, whereas tadpoles were identified to family. We noted the

minimum temperature of the night before each data collection, obtained from Environment Canada (<http://climate.weatheroffice.gc.ca>).

We conducted one trapping session of two consecutive days in each of the 2009 and 2010 field seasons (21 July 2009–15 August 2009, 18 June 2010–15 July 2010). Sites within a geographical region were visited in a random sequence in any given season. With the repeated visits from this design, we could estimate the influence of wetland and landscape-scale variables on abundance and associated dynamic parameters after accounting for imperfect detection probability (Royle and Dorazio 2008; Dail and Madsen 2011).

### Pond and landscape variables

We measured different variables at the wetlands. We used relevés to estimate the percent cover of common reed and cattail (*Typha latifolia*, *T. angustifolia*, and possibly *Typha x glauca*) at each wetland and at every amphibian sampling station (see “Amphibian sampling” section). Most of the *Typha* were *Typha angustifolia* L. (narrow-leaved cattail), but some were occasionally mixed with *Typha latifolia* L. (broad-leaved cattail). Many individuals showed intermediate characters, suggesting hybridization (*Typha x glauca* Godr.). Identification to species (or hybrid) without genetic analysis is virtually impossible for some intermediate plants. For the purposes of the study, we grouped all *Typha* irrespective of species. We also considered the percent cover of emergent plants, excluding cattail and reed. Vegetation sampling occurred during the summer of 2009, when the aerial structures of the species were well developed and easy to observe. We recorded hydroperiod data at each station (i.e., water present or absent) during the funnel trapping sessions.

To assess the effect of landscape structure on amphibian patterns, we computed landscape metrics in a geographic information system using ArcGIS 9.3 (ESRI 2008). We obtained spatial data from Natural Resources Canada, the Québec Ministry of Natural Resources, and wetland cartographies of Ducks Unlimited Canada. Based on amphibian movement distances, we created buffers of 100, 500, and 1,000 m around each wetland. We extracted the landscape cover data for forest, water, and heavily-managed areas. Heavily-managed areas consisted of residential areas, parking lots, agricultural fields, and roads. We

also computed the total length of roads within the above-mentioned buffers. We measured the distance from each wetland to the nearest forest, water, and heavily-managed area.

### Statistical analyses

In all the analyses, we used a model selection and multimodel inference approach based on the second-order Akaike information criterion ( $AIC_c$ ; Burnham and Anderson 2002). We checked the collinearity among numeric variables and did not include any variables with a Pearson  $|r| > 0.7$  in the same model. To avoid problems of model convergence, we centered numeric variables by subtracting the mean from each value before analysis (Kleinbaum et al. 1998). All analyses were performed in R 2.15.2 (R Core Team 2012). We computed  $AIC_c$ ,  $\Delta AIC_c(\Delta_i)$ , Akaike weights ( $w_i$ ) as well as model-averaged parameter estimates ( $\hat{\beta}$ ) with the AICcmodavg package (Burnham and Anderson 2002; Mazerolle 2012). We present the analytical approach along with the candidate models used to test our biological hypotheses for each of our data sets in the following sections.

### Probability of reed invasion

We used classic logistic regression to estimate the probability of reed invasion in the wetlands (assessed in 2009) as a function of local wetland characteristics, landscape cover and configuration variables. We formulated 16 models. These included a null model (intercept only), a wetland area and cattail cover model, a configuration model, as well as a natural cover model and anthropic cover model (Table 1). Other models combined wetland variables with either landscape cover or configuration variables. We repeated the 16 models for each of the three spatial scales considered (Table 1). Model fit was assessed with the Hosmer and Lemeshow as well as the Le Cessie and van Houwelingen goodness-of-fit tests (Hosmer and Lemeshow 1989; Le Cessie and van Houwelingen 1991).

### Probability of station desiccation

We assessed the effect of different variables on the probability of desiccation at the sampling stations

**Table 1** Candidate set of logistic regression models with wetland and landscape-scale variables for the reed invasion at 50 wetlands in the Montréal area, Canada

Model	Biological hypotheses
Intercept only	Null model
Wetland characteristics	
Wetland area + cattail	Effects of wetland area and cattail cover
Landscape cover <sup>a</sup>	
Forest.cov + wetland.cov	Effect of natural cover within a given radius
Lin.road + perturb.cov	Effect of length of road and cover of heavily-managed area
Landscape configuration	
Dist.forest + dist.wetland + dist.perturb	Effect of distance to natural and heavily-managed areas
Combined models	
Landscape cover + wetland characteristics	Combined effects of landscape cover and local effects
Landscape configuration + wetland characteristics	Combined effects of landscape configuration and local effects

<sup>a</sup> Models repeated for each of three radii (100, 500, and 1,000 m)

throughout the two field seasons using logistic regression with random intercepts (Zuur et al. 2009). Here, we treated each wetland and station nested within wetland as random effects. For this analysis, we considered five candidate models that consisted of: (1) the percent cover of reed, Julian date, and sampling year (hereafter, the main effects model), (2) main effects with interaction between reed cover and Julian date, (3) main effects with interaction between reed cover and year, (4) main effects with interaction between Julian date and year, (5) a null model with random intercepts (no fixed effects). Parameters were estimated with the Laplace approximation to the likelihood in R with the lme4 package (Bates et al. 2012).

#### *Amphibian abundance dynamics*

Our trapping data followed a robust design where each sampling season was considered a primary period, and with two secondary periods (nights) within each primary period (e.g., Pollock 1982). We used dynamic *N*-mixture models (Dail and Madsen 2011) to estimate the abundance of the initial year ( $\lambda_{2009}$ ), the

recruitment rate ( $\gamma$ ), the apparent survival probability ( $\omega$ ), and the detection probability of individuals ( $p$ ). Here, apparent survival denotes the complement of emigration and mortality. This approach consists in using counts of unmarked individuals collected in a given season at a suite of sites. Dynamic *N*-mixture models estimate the abundance at each site, as well as parameters describing changes in abundance across seasons (i.e.,  $\gamma$  and  $\omega$ ), after accounting for imperfect detectability. Our model assumes that the abundance at a site does not change between the two consecutive nights of trapping in a given season, and that the abundance, the rate of recruitment, as well as the probabilities of apparent survival and detection are modeled appropriately with covariates. The model also assumes that detections within each site are independent across visits, and that the abundance follows a Poisson distribution.

We tallied the total number of individuals captured for each life stage and species (or family for tadpoles) across all sampling stations of a given site on a given day. These counts formed the data in the *N*-mixture models. We analyzed data separately for adults and juveniles of each species. For each species, we formulated 19 hypotheses involving wetland characteristics and landscape variables on abundance, recruitment, and apparent survival (Table 2). To minimize the number of parameters estimated, we considered the following scenarios on either abundance, recruitment rate, or apparent survival: (1) additive effects of reed presence and wetland area (wetland additive model), (2) interactive effects of reed presence and wetland area (wetland interaction model), (3) landscape configuration model, (4) landscape cover within 100 m, (5) landscape cover within 500 m, and (6) landscape cover within 1,000 m. The landscape configuration model included the distance of each wetland relative to the closest forest, water, and heavily-managed areas (agricultural, urban, or road). Landscape composition models included the cover of forest habitat and that of heavily-managed areas (agricultural and urban cover combined) within a given radius of the three radii (e.g., 100, 500, and 1,000 m).

For each scenario on the demographic parameters described above, we tested three hypotheses on detection probability ( $p$ ): (1) additive effects of sampling effort (number of sampling stations at a given wetland), minimum air temperature on the night before trap checking, and year, (2) additive effect of

**Table 2** Candidate set of dynamic *N*-mixture abundance models with wetland and landscape-scale variables for the amphibian data at 50 wetlands in the Montréal area, Canada in 2009 and 2010

Model	Biological hypotheses
Effects on initial abundance ( $\psi$ )	
$\lambda_{\text{reed+wetland.area}} \cdot \omega \cdot P_{\text{year+airtemp+effort}}$	Abundance varies with reed presence and wetland area
$\lambda_{\text{reed+wetland.area+reed:wetland.area}} \cdot \omega \cdot P_{\text{year+airtemp+effort}}$	Effect of wetland area on abundance varies with reed presence
$\lambda_{\text{dist.water+dist.forest+dist.perturb}} \cdot \omega \cdot P_{\text{year+airtemp+effort}}$	Abundance varies with distance to landscape elements
$\lambda_{\text{forest.cov+perturb.cov}} \cdot \omega \cdot P_{\text{year+airtemp+effort}}^a$	Abundance varies with cover within a given radius
Effects on recruitment rate ( $\gamma$ )	
$\lambda_{\text{reed+wetland.area}} \cdot \omega \cdot P_{\text{year+airtemp+effort}}$	Recruitment rate varies with reed presence and wetland area
$\lambda_{\text{reed+wetland.area+reed:wetland.area}} \cdot \omega \cdot P_{\text{year+airtemp+effort}}$	Effect of wetland area on recruitment rate varies with reed presence
$\lambda_{\text{dist.water+dist.forest+dist.perturb}} \cdot \omega \cdot P_{\text{year+airtemp+effort}}$	Recruitment rate varies with distance to landscape elements
$\lambda_{\text{forest.cov+perturb.cov}} \cdot \omega \cdot P_{\text{year+airtemp+effort}}^a$	Recruitment rate varies with cover within a given radius
Effects on apparent survival ( $\omega$ )	
$\lambda_{\text{reed+wetland.area}} \cdot \gamma \cdot P_{\text{year+airtemp+effort}}$	Apparent survival varies with reed presence and wetland area
$\lambda_{\text{reed+wetland.area+reed:wetland.area}} \cdot \gamma \cdot P_{\text{year+airtemp+effort}}$	Effect of wetland area on apparent survival varies with reed presence
$\lambda_{\text{dist.water+dist.forest+dist.perturb}} \cdot \gamma \cdot P_{\text{year+airtemp+effort}}$	Apparent survival varies with distance to landscape elements
$\lambda_{\text{forest.cov+perturb.cov}} \cdot \gamma \cdot P_{\text{year+airtemp+effort}}^a$	Apparent survival varies with cover within a given radius
Null model	
$\lambda \cdot \omega \cdot \gamma \cdot p$	All parameters are constant

<sup>a</sup> Models repeated for each of three radii (100, 500, and 1,000 m). Note that subscripts indicate the covariates included on each parameter and that a dot (e.g.,  $\lambda_{\cdot}$ ) denotes a parameter that is held constant. Six scenarios on detection probability were considered for each hypothesis (see text for details)

minimum air temperature and interactive effects of effort and year, (3) additive effect of sampling effort and interactive effects of minimum air temperature and year. Thus, we considered 57 models to test our hypotheses (i.e., 19 scenarios on population parameters  $\times$  three scenarios on detectability). Reviewers suggested to include models with the effects of precipitation on detection probability. To address reviewer concerns, we obtained total precipitation 24 h before trap checking from Environment Canada (<http://climate.weatheroffice.gc.ca>). We included this variable on three new scenarios (i.e., 57 models) on detection probability: (1) additive effects of sampling effort, total precipitation 24 h before trap checking, and year, (2) additive effect of total precipitation and interactive effects of effort and year, (3) additive effect of sampling effort and interactive effects of total precipitation and year. We contrasted these models against a null model that considered all parameters constant ( $\lambda \cdot \omega \cdot \gamma \cdot p$ ).

Rapid tadpoles were analyzed as a single group as they could not be identified to species in the field.

Tadpoles captured in our traps were of size classes near metamorphosis. We modeled their abundance assuming complete turnover between the 2 years. This assumption seemed appropriate in our case as tadpoles reaching metamorphosis are not available for capture as tadpoles the next year. We implemented this model by using single season *N*-mixture models (Royle 2004), where we modeled abundance with a zero-inflated Poisson distribution. In this case, we included a year factor on abundance in all models. We considered the same scenarios on abundance and on detection probability as for the adult and juvenile analyses above. We also included a null model with both abundance and detectability constant, for a total of 19 models (Table 2).

We tested the fit of the top-ranked *N*-mixture models with a parametric bootstrap approach based on the  $\chi^2$  statistic and 5,000 bootstrap samples. Parameter estimates were obtained by maximum likelihood using the unmarked package (Fiske et al. 2012) and model selection was implemented with the AICcmodavg package (Mazerolle 2012).

## Results and discussion

Forty-five wetlands (91 %) retained water during our sampling seasons, although some sampling stations dried up. Reed cover in invaded wetlands ranged between 1 and 64 %, with a mean  $\pm$  SD of  $27.8 \pm 18.7$  %. Cattail covered 0–93.4 % of wetland surface area. Forest and water cover around wetlands in buffers of 100, 500, and 1,000 m, ranged between 8.9 and 100 %, whereas the cover of heavily-managed areas in these buffers ranged from 0 to 91.1 %. The distance between heavily-managed areas and wetlands varied between 0 and 356 m. In contrast, forested areas were between 0 and 1,085 m from wetlands.

### Probability of reed invasion

There was no indication of lack of fit for the models. Both the Hosmer and Lemeshow and Le Cessie and van Houwelingen tests produced  $P > 0.11$ . There was considerable model selection uncertainty among the reed invasion models, with four models having  $\Delta_i < 2$ . The highest-ranked model consisted of the length of roads and cover of heavily-managed areas within 1,000 m of the wetland and was followed very closely by a second model combining the same two variables with wetland area and cattail cover (Table 3). The third-ranked model consisted of the distance to landscape elements, whereas a fourth model included the wetland area and cattail cover. The probability of reed invasion in wetlands marginally increased with the cover of heavily-managed areas within 1,000 m ( $\hat{\beta} = 2.94$ , 95 % CI :  $-0.03, 5.91$ ; Fig. 2a), but decreased with the length of roads within 1,000 m ( $\hat{\beta} = -0.08$ , 95 % CI :  $-0.16, 0.01$ ; Fig. 2b). The probability of reed invasion also tended to increase with the distance to the nearest forest ( $\hat{\beta} = 3.76$ , 95 % CI :  $-0.31, 7.84$ ; Fig. 2c). In contrast, reed invasion probability did not vary with wetland area, cattail cover, distance to nearest heavily-managed area, and distance to nearest water.

We predicted that reed invasion would increase with anthropic disturbances such as habitat loss through urban expansion. The probability of reed invasion in a wetland increased with the percent cover of heavily-managed areas within 1,000 m. This result was consistent with our hypothesis. Similarly, Chambers et al. (1999), Bart et al. (2006), and Silliman and

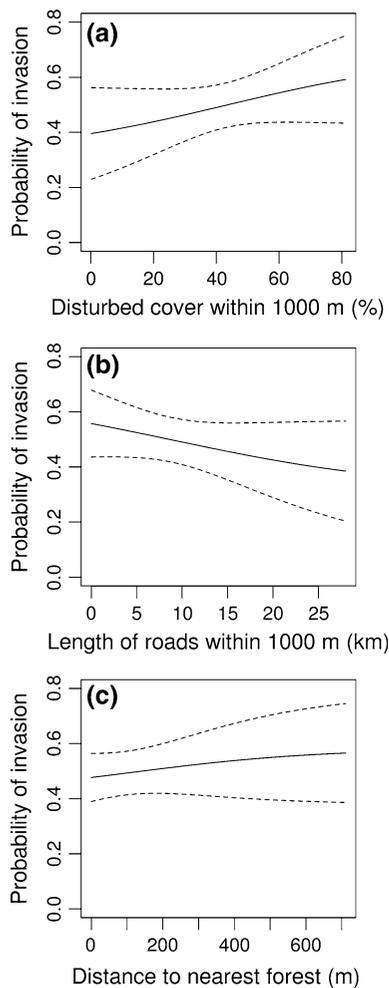
**Table 3** Top-ranked logistic regression models ( $\Delta_i < 2$ ) of reed invasion and station desiccation at 50 wetlands of the Montréal area, Québec, Canada

Model	$K$	AIC <sub>c</sub>	$\Delta_i$	$w_i$
Probability of reed invasion				
Lin.road1000 + perturb.cov1000	3	68.78	0.00	0.22
Lin.road1000 + perturb.cov1000 + wetland.area + cattail	5	69.56	0.79	0.15
Dist.forest + dist.wetland + dist.perturb	4	69.85	1.08	0.13
Wetland.area + cattail	3	69.94	1.16	0.12
Probability of station desiccation				
Reed.cover + Julian.day + Year + Year:Julian.day	7	1,548.08	0.00	1
Reed.cover + Julian.day + Year + Year:Reed.cover	7	1,575.19	27.11	0
Reed.cover + Julian.day + Year	6	1,591.03	42.95	0
Reed.cover + Julian.day + Year + Reed.cover:Julian.day	7	1,591.86	43.78	0
Null model	3	1,750.53	202.45	0

Note that  $K$ ,  $\Delta_i$ , and  $w_i$  denote the number of estimated parameters, the difference in AIC<sub>c</sub> relative to the top model, and the Akaike weights, respectively

Bertness (2004) noted that common reed is closely associated with areas undergoing anthropic disturbances. We also observed that the probability of reed invasion increased with the distance to the nearest forest. Shoreline areas where woody vegetation has been removed tend to have greater cover of common reed (Silliman and Bertness 2004). Common reed is a wetland species thriving in open areas, and there is evidence that trees can impose barriers to reed dispersal (Brisson et al. 2010). Our results support the latter hypothesis.

Surprisingly, we found that the probability of reed invasion decreased with increasing length of roads within 1,000 m. This result was unexpected, because reeds disperse along road corridors (Lelong et al. 2007; Brisson et al. 2010). The type of road, road width, and surface deposit may also influence the occurrence of common reed along roads, with a greater probability of reed establishment along highways (Lelong et al. 2009). In our case, we did not record data on the previously-mentioned road



**Fig. 2** Model-averaged probability of reed invasion in wetlands of the Montréal area, Canada. Dotted lines indicate unconditional standard errors around predictions

attributes, which could explain the discrepancies we report.

#### Probability of desiccation

Out of the 455 sampling stations, 126 dried at least once during our two sampling seasons. There were similar amounts of precipitations and mean temperatures during the two field seasons (339 mm and 18 °C in 2009, 379 mm and 20 °C in 2010). The model with the interaction between year and date had the entire support (Table 3). The probability of the station drying out increased with reed cover ( $\hat{\beta} = 1.87$ , 95 % CI : 0.47, 3.28). Furthermore, the

probability of desiccation increased with Julian date in 2010, but did not vary with Julian date in 2009 ( $\hat{\beta} = 0.04$ , 95 % CI : 0.03, 0.06).

We predicted that increasing reed cover would reduce habitat quality by increasing the desiccation rate at sampling stations. As expected, the probability of desiccation at a station increased with the reed cover. Our results are consistent with Chambers et al. (1999). Common reed has a high transpiration rate which can decrease the water level (Burba et al. 1999; Windham and Lathrop 1999). A reduction in water level would primarily influence tadpole development, as shortening the hydroperiod can reduce the time to metamorphosis (Laurila and Kujasalo 1999). Early metamorphosis at a smaller size can induce a lower post-metamorphic survival rate compared to development under longer hydroperiods (Laurila and Kujasalo 1999; Altwegg and Reyser 2003).

#### Abundance dynamics

We captured an average of 15.3 and 14.9 anurans (adults and juveniles) per 100 trap nights in 2009 and 2010, respectively, where one trap night equates to one trap open for one night. We caught potential predators of amphibians including fish, leeches, giant water bugs (*Belostoma* sp.), diving water beetles (*Dytiscus* sp.), dragonfly larvae (*Aeshna* sp.), and water scorpions (*Ranatra fusca*). Due to the high aquatic predator occurrence and low variability among wetlands (80–96 % of the wetlands), we could not include these variables in our analyses.

We trapped an average of 89.8 and 47.1 ranid tadpoles per 100 trap nights in 2009 and 2010, respectively. Most of the anurans captured were green frogs and leopard frogs. No American toads or western chorus frogs were caught. Green frog and leopard frog captures were sufficient to attempt analyses for each of their life stages (tadpoles, juveniles, and adults). Our goodness-of-fit test with 5,000 iterations indicated that *N*-mixture models fit the data for most groups (*P* between 0.24 and 0.26), except for adult leopard frogs and juvenile green frogs for which the fit was marginal (*P* = 0.06 and 0.04, respectively).

For most groups, models including landscape-scale variables on population parameters ranked as well or higher than those with wetland-scale variables (Table 4). The effect of landscape variables on

**Table 4** Top-ranked dynamic  $N$ -mixture abundance models ( $\Delta_i < 2$ ) on trapping data of anurans at 50 wetlands of the Montréal area, Québec, Canada in 2009 and 2010

Model	$K$	$AIC_c$	$\Delta_i$	$w_i$
<b>Juvenile green frogs</b>				
$\lambda$ . $\gamma$ . $\omega$ .forest.cov500+perturb.cov500 $P_{\text{year+effort+prec}}$	9	428.81	0.00	0.44
<b>Adult green frogs</b>				
$\lambda$ .reed+wetland.area $\gamma$ . $\omega$ . $P_{\text{year+effort+prec+year:effort}}$	10	285.85	0.00	0.21
$\lambda$ .reed+wetland.area $\gamma$ . $\omega$ . $P_{\text{year+effort+prec}}$	9	285.92	0.07	0.21
$\lambda$ .reed+wetland.area $\gamma$ . $\omega$ . $P_{\text{year+effort+airtemp}}$	9	286.36	0.51	0.17
$\lambda$ .reed+wetland.area $\gamma$ . $\omega$ . $P_{\text{year+effort+airtemp+year:effort}}$	10	286.80	0.95	0.13
<b>Juvenile leopard frogs</b>				
$\lambda$ .forest.cov100+perturb.cov100 $\gamma$ . $\omega$ . $P_{\text{year+effort+prec+year:prec}}$	10	236.21	0.00	0.53
<b>Adult leopard frogs</b>				
$\lambda$ . $\gamma$ .forest.cov500+perturb.cov500 $\omega$ . $P_{\text{year+effort+airtemp}}$	9	120.92	0.00	0.38
$\lambda$ . $\gamma$ .forest.cov500+perturb.cov500 $\omega$ . $P_{\text{year+effort+prec+year:eff}}$	10	121.90	0.97	0.23
$\lambda$ . $\gamma$ .forest.cov500+perturb.cov500 $\omega$ . $P_{\text{year+effort+prec+year:prec}}$	10	122.06	1.14	0.22
$\lambda$ . $\gamma$ . $\omega$ . $p$ .	4	122.53	1.61	0.17
<b>Ranid tadpoles</b>				
$\lambda$ .year+forest.cov500+perturb.cov500 $P_{\text{year+effort+airtemp+year:airtemp}}$	10	1,122.29	0.00	0.91

Note that  $K$ ,  $\Delta_i$ , and  $w_i$  denote the number of estimated parameters, the difference in  $AIC_c$  relative to the top model, and the Akaike weights, respectively. Subscripts in models indicate the covariates included on parameters  $\lambda$ ,  $\gamma$ ,  $\omega$ ,  $p$ , denoting abundance in the first year, recruitment rate, apparent survival probability, and probability of detection, respectively

abundance and vital rates varied across groups. The highest-ranked models for juvenile green frogs included the effect of landscape cover on annual apparent survival and constant abundance and recruitment rate. Annual apparent survival of juvenile green frogs increased with the cover of heavily-managed areas within 500 m ( $\hat{\beta} = 18.22$ , 95 % CI : 2.27, 34.17; Fig. 3a). For adult green frogs, the top-ranked models consisted of wetland characteristics on abundance with constant recruitment rate and annual apparent survival (Table 4). The abundance of adult green frogs in 2009 was greater in wetlands invaded by reeds than in wetlands without reeds ( $\hat{\beta} = 1.17$ , 95 % CI : 0.29, 2.05; Fig. 3b). Furthermore, the abundance of adult green frogs in 2009 decreased with increasing wetland area ( $\hat{\beta} = -1.72$ , 95 % CI : -3.32, -0.13; Fig. 3c).

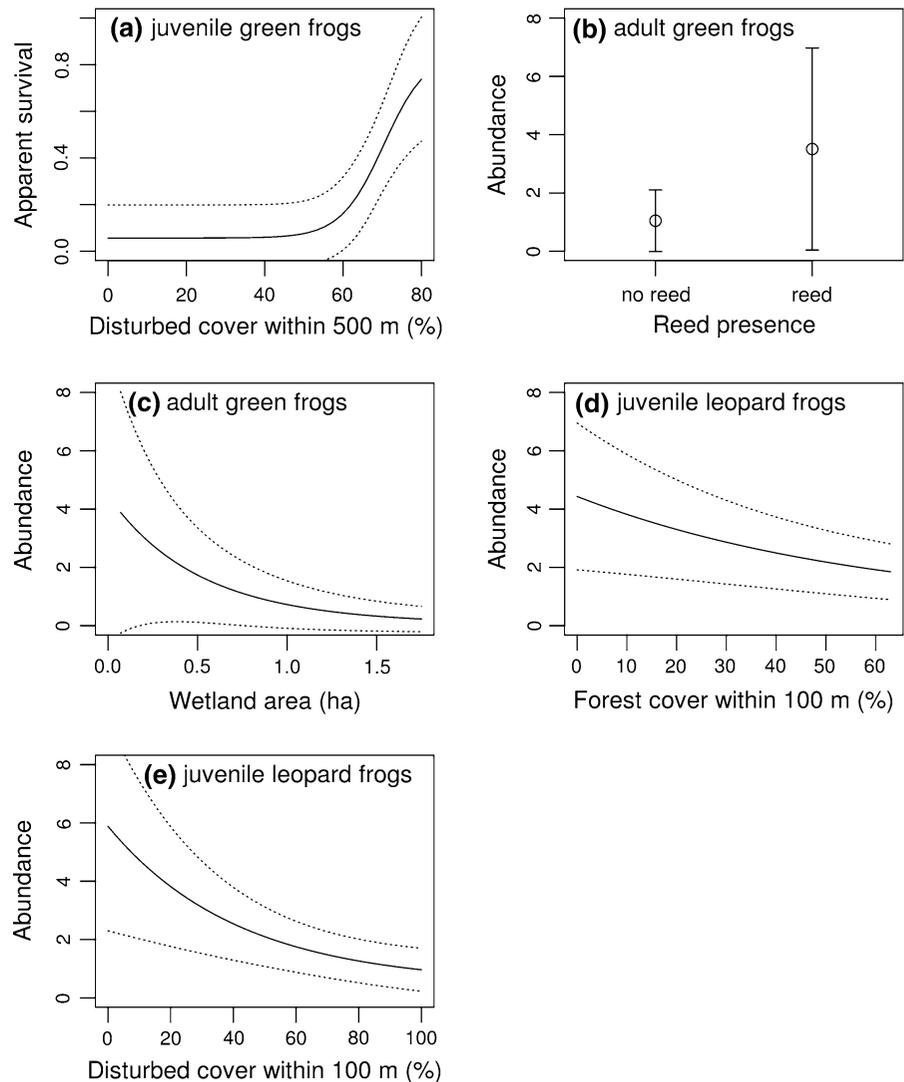
The top-ranked models for juvenile leopard frogs consisted of landscape cover within 100 m on the abundance of the first year, and constant rate of recruitment and apparent annual survival (Table 4). The abundance of juvenile leopard frogs in 2009 decreased with increasing forest cover within 100 m ( $\hat{\beta} = -1.69$ , 95 % CI : -2.98, -0.39; Fig. 3d) and the

cover of heavily-managed areas within 100 m ( $\hat{\beta} = -2.41$ , 95 % CI : -3.78, -1.04; Fig. 3e). The top-ranked model for adult leopard frogs consisted of landscape cover variables within 500 m on recruitment rate, with constant abundance and apparent survival. However, this model was followed closely by the null model ( $\Delta_i = 1.61$ , Table 4). None of the population parameters of adult leopard frogs varied with the variables we considered.

For ranid tadpoles, the model consisting of landscape cover within 500 m on abundance was the most parsimonious and had almost all of the support ( $w_i = 0.91$ , Table 4). The abundance of this group increased with the amount of forest cover within 500 m ( $\hat{\beta} = 2.35$ , 95 % CI : 1.79, 2.90; Fig. 4a) and the cover of heavily-managed areas within 500 m ( $\hat{\beta} = 3.39$ , 95 % CI : 2.86, 3.92; Fig. 4b). The abundance of ranid tadpoles was greater in 2010 than 2009 ( $\hat{\beta} = 0.87$ , 95 % CI : -0.02, 1.75).

We hypothesized that amphibian abundance and vital rates in wetlands would be lower in the presence of common reed. In a recent review, Martin and Murray (2011) predicted that the establishment of

**Fig. 3** Model-averaged population parameters of juvenile and adult frogs in wetlands of the Montréal area, Canada. Dotted lines indicate unconditional standard errors around predictions

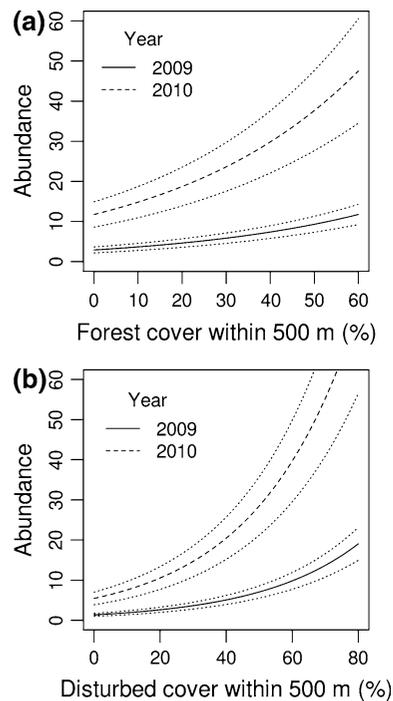


exotic plants could negatively impact anuran habitat use, species diet and interactions, and reproductive success. However, we found no negative effects of reed presence on the demographic parameters we considered. In fact, the abundance of adult green frogs in 2009 was greater in wetlands invaded by reed than in wetlands without reed. In an observational field study, Meyer (2003) observed amphibian juveniles and adults in reed stands, but did not detect tadpoles in these habitats. In our case, we detected all life stages at capture stations among reed stands.

Cohen et al. (2012) observed no differences in the development of tadpoles reared in habitats dominated by either native plants or exotic plants including

common reed. Two field studies focusing on adult amphibians report negative effects of invasive plant species. Watling et al. (2011b) report lower amphibian species richness in plots invaded by *Lonicera maackii* than in uninvaded plots, potentially related to low temperatures induced by the presence of *L. maackii*. Maerz et al. (2005b) observed that the invasive Japanese knotweed (*Fallopia japonica*) reduces foraging success of adult *L. clamitans*.

Based on the reports published so far, common reed invasion would mostly influence the larval period. Indeed, Perez et al. (2013) observed that wood frog (*L. sylvaticus*) tadpoles developed more slowly under medium and high reed densities than under a control.



**Fig. 4** Model-averaged abundance of ranid tadpoles in wetlands of the Montréal area, Canada. Dotted lines indicate unconditional standard errors around predictions

This negative effect might be offset by the reduction of the water level by common reed, though it remains to be confirmed. The results from our observational study oppose those of experiments conducted with tadpoles in mesocosms or field cages. In a study of nine wetland plant species, Cohen et al. (2012) reported negative impacts of certain plant traits, namely soluble phenolics and litter C:N ratio, on the larval development of three anuran species. These traits were independent of plant origin (native or exotic). In contrast, Rogalski and Skelly (2012) reported positive effects of reed litter on bullfrog larval development. The discrepancies between manipulative experiments and our own study suggest that reed presence has a weak effect relative to other wetland characteristics or landscape variables.

With a single exception, wetland-scale characteristics had weak effects on amphibian variables in our study. The abundance of adult green frogs in 2009 decreased with increasing wetland size. Some authors report that amphibian presence increases with pond size (Laan and Verboom 1990; Bradford et al. 2003; Hamer and Mahony 2010), whereas others indicate a

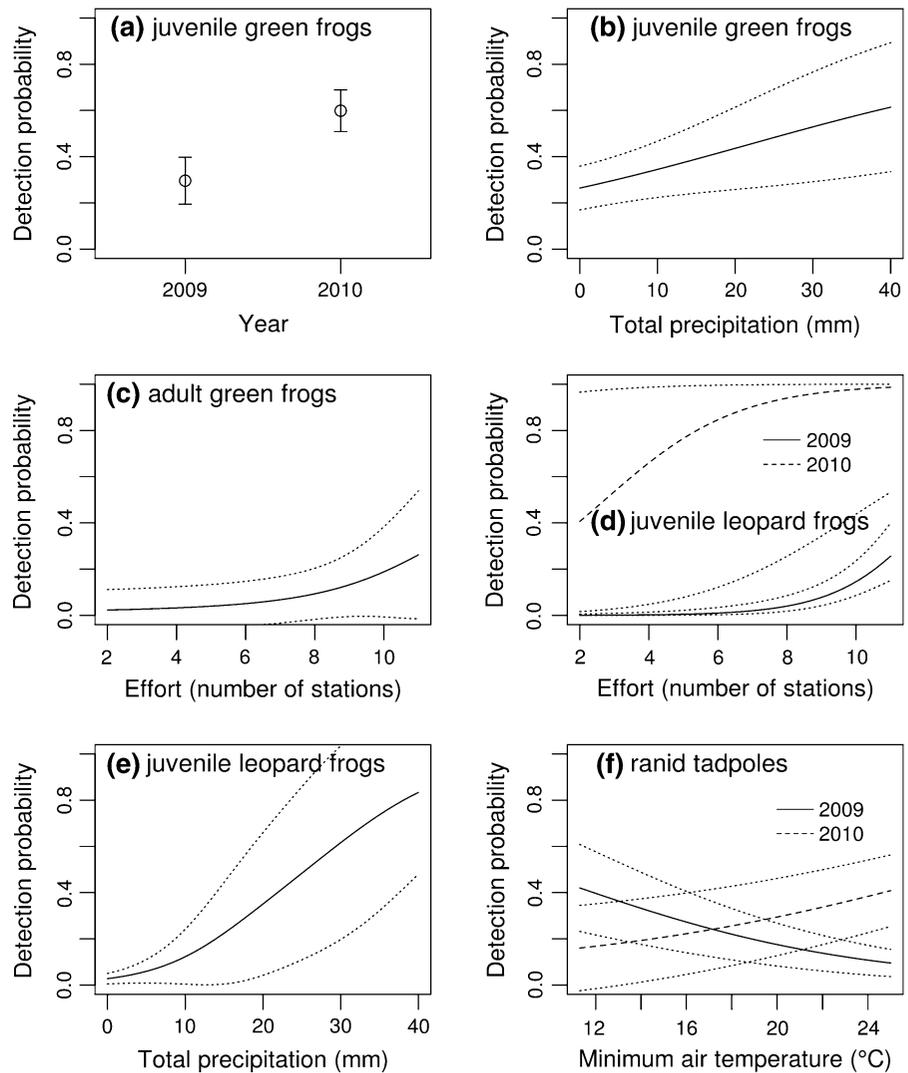
negative relationship (Knutson et al. 2004). Amphibian species richness, occupancy, and abundance can vary with a number of wetland variables such as water body depth and vegetation cover (Knapp et al. 2003; Knutson et al. 2004; Pearl et al. 2005; Hamer and Parris 2011). The presence of aquatic predators can also influence amphibian patterns, but often varies with the type of predator (Babbitt et al. 2003; Porej and Hetherington 2005; Shulse et al. 2013). Unfortunately, the high occurrence of fish and invertebrate predators in our wetlands precluded their inclusion in our analyses. The weak relationships of amphibian demographic parameters and wetland-scale variables might be due to the high urbanization in our landscape. However, this should be substantiated with a formal evaluation of interactive effects by considering landscapes with different levels of urbanization.

Landscape cover influenced the abundance or vital rates of three groups. Ranid tadpole abundance increased with the proportion of forest cover around a wetland. This suggests that forest habitat in the landscape promotes the recruitment of ranid tadpoles. Forest habitat in the vicinity of the wetland may facilitate individual movements to wetlands, as juveniles of certain species are more likely to move toward forest than open-field habitats (Rothermel and Semlitsch 2002). No adult or juvenile parameter increased with forest cover in our study, although other studies report a positive association between occurrence of pond-breeding species and forest cover or forest proximity (Hecnar and M'Closkey 1998; Guerry and Hunter 2002; Weyrauch and Grubb 2004; Hamer and Parris 2011).

Species responded differently to the cover of heavily-managed areas around wetlands. The apparent survival of juvenile green frogs increased with the cover of heavily-managed areas within 500 m of the wetland. The abundance of ranid tadpoles followed a similar pattern. In contrast, the abundance of juvenile leopard frogs in 2009 decreased with increasing cover of forest and heavily-managed areas within 100 m. Heavily-managed environments in our study consisted of residential areas, agricultural fields, and roads.

Amphibian distribution is influenced by environmental variables such as the availability of breeding, foraging, and overwintering areas (Wilbur 1980; Semlitsch 2002). The quantity, accessibility, and suitability of these habitats also determine amphibian population structure (Semlitsch 2002). Hostile

**Fig. 5** Model-averaged detection probability of different anuran life stages in wetlands of the Montréal area, Canada. Dotted lines indicate unconditional standard errors around predictions



environments in the landscape, such as those encountered in urbanized landscapes, can hinder movements of individuals (Rothermel 2004; Mazerolle and Desrochers 2005; Mazerolle and Vos 2006). For instance, roads or urban areas pose barriers to juvenile dispersal and adult seasonal migrations (Marsh et al. 2005; Andrews et al. 2008; Bouchard et al. 2009). Similarly, Knutson et al. (1999) and Hamer and Parris (2011) reported that anuran species richness decreased with the presence of urban areas or the density of residences. The expansion of heavily-managed areas in the vicinity of wetlands may concentrate individuals in wetlands in the short term, while reducing genetic diversity in the long term, though this remains speculative and should be tested formally.

Nonetheless, increasing road density ultimately lowers amphibian occupancy, abundance, and genetic diversity (Fahrig et al. 1995; Vos and Chardon 1998; Vos et al. 2001).

Adults and juveniles are the most mobile amphibian life stages. We expected that these life stages would respond to landscape-scale variables more strongly than tadpoles. Unexpectedly, we found that juveniles and tadpoles responded to landscape characteristics, but not adults. The juvenile stage is associated with dispersal and long-distance colonization events, although generally shorter than 10 km (Dole 1971; Berven and Grudzien 1990; Semlitsch 2008). Furthermore, juveniles lose water more rapidly than adults (Thorson 1955). Our results suggest that the landscape

is more permeable to adult than juvenile movements. This is consistent with higher rates of evaporative water loss and greater dispersal distances than adults. However, the interpretation of landscape variables on tadpoles is more problematic and may reflect indirect effects on adults. For instance, adults may have higher reproductive outputs when forest cover within 500 m is high, but further investigation on this issue is warranted.

### Detection probability

The detection probability of juvenile green frogs was greater in 2010 than in 2009 ( $\hat{\beta} = 1.28$ , 95 % CI : 0.13, 2.43, Fig. 5a) and marginally increased with precipitation in the previous 24 h ( $\hat{\beta} = 0.05$ , 95 % CI :  $-0.005$ , 0.096, Fig. 5b). However, detection probability of the group did not vary with sampling effort or minimum air temperature. The detection probability of adult green frogs increased marginally with sampling effort ( $\hat{\beta} = 0.23$ , 95 % CI :  $-0.02$ , 0.48, Fig. 5c), but did not vary with any other variable.

The detection probability of juvenile leopard frogs increased with sampling effort, but its effect was weaker in 2010 than 2009 (year  $\times$  effort interaction,  $\hat{\beta} = -0.91$ , 95 % CI :  $-1.60$ ,  $-0.21$ , Fig. 5d). Despite this interaction, detection probability was substantially higher in 2010 than 2009 ( $\hat{\beta} = 2.7$ , 95 % CI : 0.49, 4.91). The probability of detection of juvenile leopard frogs increased with the amount of precipitation in the previous 24 h ( $\hat{\beta} = 0.15$ , 95 % CI : 0.00, 0.30, Fig. 5e), but did not vary with air temperature. Detectability of adult leopard frogs did not vary with any of the sampling covariates we considered. The detection probability of tadpoles increased with minimum air temperature in 2010, but did not vary with the variable in 2009 ( $\hat{\beta} = 0.26$ , 95 % CI : 0.17, 0.36, Fig. 5f). Detection probability of the group did not vary with precipitation on the previous day or sampling effort.

The probability of detection varied with sampling year, minimum air temperature within 24 h, total precipitation within 24 h, and sampling effort for some species. Weather variables influence amphibian breeding activity (Obert 1976; Oseen and Wassersug 2002; Steen et al. 2013) and our reported effect of air

temperature on detectability (i.e., capture) is consistent with such patterns. As we expected, the effect of some variables on detectability varied with year, as was the case of air temperature for ranid tadpoles and juvenile leopard frogs. We included covariates known to influence detectability to improve estimates of abundance, recruitment, and apparent survival (MacKenzie et al. 2006, Royle and Dorazio 2008).

Detectability in our study was a nuisance parameter, in the sense that it must be included in the analysis, while not being the focus of the analysis. In our case, abundance dynamics were the focus of our study. During a sampling event in the field (e.g., trap open for 24 h), some individuals are likely missed (Williams et al. 2002). As a result, counts provide a minimum number of individuals present at a site during the sampling period. Counts are difficult to compare across sites without making strong assumptions about detectability being constant across habitat type, sites, season, weather conditions, sex, or sampling method (Anderson 2001; Mazerolle et al. 2007). This problem has been addressed by a large class of models in animal ecology. For example, capture–mark–recapture, distance sampling, and site occupancy models estimate the biological parameters of interest after having accounted for imperfect detectability or capture probability (Mazerolle et al. 2007; Williams et al. 2002). Such approaches provide better estimates than methods assuming that detectability is constant, allowing one to compare population parameters across studies, species, and habitats (Mazerolle et al. 2007; Williams et al. 2002).

### Conclusion

Wetlands in the vicinity of heavily-managed areas were more likely to be invaded by common reed. The probability of desiccation at stations increased with the percent cover of reed. However, we found no negative effect of reed invasion on the distribution of amphibian tadpole, juvenile, or adult life stages in our urbanized landscape. The abundance or vital rates of juvenile green frogs, juvenile leopard frogs, and ranid tadpoles varied with the amount of forest cover and heavily-managed areas within 100 and 500 m. In the context of plant invasion, the landscape surrounding breeding wetlands had a greater influence on amphibian patterns than the invasion of common reed and

wetland characteristics. The more important drivers of population dynamics in our system may be reproductive output and movements of juveniles and adults outside wetlands, rather than reed invasion.

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