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Landscape context is more important than wetland buffers for farmland amphibians

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ABSTRACT

In regions with high rates of wetland loss, remnant wetlands and constructed ponds can provide important breeding habitat for amphibians. However, such wetlands are often embedded in a matrix of agricultural fields, potentially putting species within these wetlands at risk. One recommendation for conservation of amphibians in agriculture-dominated landscapes is to maintain a buffer of permanent vegetation around the wetland. However, it is not clear how wide wetland buffers must be to effectively conserve amphibians in agriculture-dominated landscapes or what vegetation types are suitable buffer vegetation. Furthermore, it is not clear whether wetland buffers produce similar—or better—conservation outcomes for amphibians than actions conducted at larger spatial extents. We addressed these questions using data from anuran (frog and toad) breeding call surveys in 36 wetlands in rural eastern Ontario, Canada. First, we tested for the effects of 49 different wetland buffer measurements on anuran richness, relative anuran abundance, and the abundance/probability of occurrence of individual species. These 49 measurements represented all combinations of seven different ways to measure the wetland buffer size and seven types of buffer vegetation. Wetland buffer size was measured as the minimum width of buffer vegetation contiguous with the wetland and proportion of the area within 5, 16, 30, 50, 120, or 300 m of the wetland containing buffer vegetation that was contiguous with the wetland. Then, to compare the strength of effect of wetland buffers versus landscape context on anurans, we compared the wetland buffer measurement with the strongest positive effect on each anuran response (from the previous analysis) to the effects of three landscape-scale variables: area of woodland; area of wetlands, streams, rivers, and lakes; and road density. We did not detect positive effects of wetland buffers on anuran richness or relative anuran abundance. This is because positive effects of wetland buffers on individual species were rare, i.e. positive effects were only supported for two of the six species with enough data to model individually: American toads (*Anaxyrus americanus*) and green frogs (*Lithobates clamitans*). Furthermore, we found that the landscape context had much stronger effects on relative anuran abundance than the wetland buffer, with effect sizes ranging from 4 (road density) to 14 (woodland cover) times that of the wetland buffer. These findings suggest that guidelines for anuran conservation in agricultural landscapes should generally focus on protection of terrestrial habitat at the landscape scale rather than on maintenance of wetland buffers.

1. Introduction

Wetland loss has been implicated in global declines in amphibian abundance and diversity. For example, a meta-analysis found that amphibian abundance was consistently lower in landscapes with less wetland cover than in landscapes with more wetland cover (Quesnelle et al., 2015). Similarly, amphibian richness has been shown to increase with the total amount of wetland in the landscape (e.g. Houlahan and Findlay, 2003). The importance of wetlands for amphibians is not surprising, given that many require freshwater habitat for at least part of their life cycles.

Most wetland loss has occurred through conversion of wetlands to agricultural fields. In their global meta-analysis of the causes of wetland loss, van Asselen et al. (2013) found that cropland expansion was responsible for 58% of documented wetland losses. In Europe and North America—which have experienced the largest overall losses of wetland (Davidson, 2014)—50% of ponds, small lakes, inland marshes, and coastal marshes were converted to intensive agricultural land between 1900 and 1985, approximately halving the breeding habitat available to amphibians (Millennium Ecosystem Assessment, 2005).

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In regions with high rates of wetland loss, remnant wetlands and constructed ponds can provide important breeding habitat for amphibians (e.g. Collins and Fahrig, 2017; Knutson et al., 2004). However, such wetlands are often embedded in a matrix of agricultural and other human-dominated land cover types, potentially putting species within these wetlands at risk.

One recommendation for conservation of amphibians in agriculture-dominated landscapes is to maintain a buffer of permanent vegetation surrounding the wetland (e.g. Coukell et al., 2004). Such wetland buffers may benefit amphibians by providing habitat for species that require terrestrial habitat for some portion of their life cycle. For example, amphibian richness and species occurrence often increase with the amount of woodland cover in the surrounding area (e.g. Collins and Fahrig, 2017; Findlay et al., 2001; Herrmann et al., 2005; Houlahan and Findlay, 2003; Koumaris and Fahrig, 2016). Wetland buffers may also improve water quality. For example, Madison et al. (1992) found that vegetated riparian buffers 30 m in width could trap up to 99% of atrazine and nitrate in agricultural run off. Such pesticides and fertilizers can have negative effects on amphibian survival and growth rates in agricultural wetlands (Baker et al., 2013).

However, it is not clear how large wetland buffers must be to effectively conserve amphibians in agriculture-dominated landscapes. Most recommended buffer widths in North America, for example, are ≤ 30 m (Coukell et al., 2004; Ontario Farm Environmental Coalition, 2004). However, population viability analyses have suggested that these buffers are not wide enough to provide the terrestrial habitat needed to support viable amphibian populations (Harper et al., 2008). Mark-recapture, radiotelemetry, and genetic studies suggest that amphibians frequently move and forage within 300 m of their breeding habitat (Baldwin et al., 2006; Forester et al., 2006; Semlitsch, 2008; Semlitsch and Bodie, 2003). Thus buffers may need to be at least 300 m wide to adequately protect terrestrial habitat for wetland-breeding amphibians. Wider buffers may also be needed to mitigate fertilizer and pesticide use in the surrounding landscape. For example, Sawatzky (2016) found that the strongest effects of land cover (e.g. woodland cover, row crop cover) on pesticide concentrations in ponds typically occurred when land cover was measured within at least 150 m of ponds. This suggests that buffers may need to be at least 150 m wide to effectively reduce pesticide levels in wetlands. To our knowledge, no empirical studies to date have investigated how wide wetland buffers must be to benefit amphibians in agricultural environments.

Additionally, it is not clear whether wetland buffers, by virtue of being contiguous with wetland edges, produce better conservation outcomes for amphibians than conservation actions conducted at larger spatial extents. Many studies have shown that amphibians can be affected by the landscape context of a wetland (e.g. woodland cover, wetland cover, road density in the surrounding landscape) at scales much larger than even the maximum government-recommended buffer width of 300 m in our study region (Ontario; Coukell et al., 2004; Ontario Farm Environmental Coalition, 2004), i.e. within 500–3000 m of breeding wetlands (e.g. Findlay et al., 2001; Hartel et al., 2010; Herrmann et al., 2005; Houlahan and Findlay, 2003; Jeliazkov et al., 2014; Rubbo and Kiesecker, 2005). Such effects may occur, at least in part, because water quality is affected by the surrounding landscape context. For example, Houlahan and Findlay (2004) found effects of forest cover on water nutrient levels up to 4 km from the wetland edge. Such effects may also occur because juvenile and adult amphibians interact with (and are thus affected by) the landscape context during dispersal from their natal/breeding pond, and such dispersal movements may cover several km (Baldwin et al., 2006; Forester et al., 2006; Semlitsch, 2008; Semlitsch and Bodie, 2003). Additionally, some amphibians may be affected by the landscape context of a wetland because they overwinter in terrestrial habitats (Semlitsch and Bodie, 2003).

We conducted breeding call surveys for frogs and toads (i.e. anurans) in 36 wetlands in agriculture-dominated landscapes in rural eastern Ontario, Canada, to address the following questions:

(1) Can wetland buffers increase anuran species richness and relative abundance in agricultural wetlands? And, if so, how wide should these buffers be?
(2) How strong are wetland buffer effects on anurans, relative to the effects of the landscape context of the wetland, i.e. woodland cover, water cover, and road density in the surrounding landscape?

2. Methods

2.1. Overview

To determine if wetland buffers can benefit amphibians in agriculture-dominated landscapes, we tested for relationships between each anuran response—anuran richness, relative anuran abundance (i.e. the combined abundance across species), and the abundance/occurrence of individual species—and 49 different measurements of the wetland buffer size across 36 sample landscapes in rural eastern Ontario, Canada (Fig. 1). We measured the wetland buffer size in two ways, either as (a) the minimum width of suitable buffer vegetation contiguous with the edge of the study wetland, or (b) the proportion of the area within 5, 16, 30, 50, 120, or 300 m of the wetland containing buffer vegetation that was contiguous with the wetland (Fig. 2). Thus in the second approach we tested for effects of wetland buffer size on anurans within six recommended buffer widths. We accounted for uncertainty in the type (s) of suitable vegetation for a wetland buffer (e.g. all permanent vegetation or woodland only) by making each of the above seven measurements for each of seven types of wetland buffer vegetation.

To compare the strength of effect of the wetland buffer size versus landscape context on anurans, we compared the 'best' wetland buffer measurement—the one with the strongest positive effect on an anuran response (from the analyses above)—to the effects of three landscape-scale variables: woodland cover (the area of woodland within the landscape, divided by the total landscape area), water cover (the area of wetlands, streams, rivers, and lakes within the landscape, divided by the landscape area), and road density (the total length of roads within the landscape, divided by the landscape area). To select the appropriate landscape scale for these measurements, we first tested relationships between each anuran response and each landscape variable measured at four landscape scales, i.e. the area within 0.5, 1, 1.5, or 2 km of the edges of the sampled wetlands. In tests comparing the effects of the wetland buffer to the effects of landscape-scale variables on anuran responses, we included each landscape variable at its 'scale of effect,' defined as the landscape scale that produced the strongest relationship with each anuran response. The relative strengths of the relationships between an anuran response and wetland buffer size, woodland cover, water cover, and road density were measured as the model-averaged, standardized slopes of the relationships, based on model selection using the small-samples Akaike Information Criterion (AICc).

2.2. Site selection

All study wetlands were located in rural eastern Ontario, Canada, which is in the easternmost portion of the Lake Simcoe-Rideau Ecoregion (Fig. 1; Crins et al., 2009). Land use in eastern Ontario is dominated by agriculture, with ~ 63% of farmland used for crop production (primarily corn, soybean, and hay) and ~ 15% used as pasture for livestock (OMAFRA, 2016). The dominant natural land cover type in the region is woodland.

We selected 36 study wetlands (Fig. 1). Wetlands were primarily selected to maximize variation in the size of the wooded wetland buffer and landscape-scale woodland cover while minimizing the correlation between these variables. During site selection, the size of the wooded wetland buffer was measured as the woodland area contiguous with wetland edges using aerial photographs (Google, 2015; OMNR, 2009). Landscape-scale woodland cover was measured as the total woodland cover within a 1-km radius of potential study wetlands, irrespective of

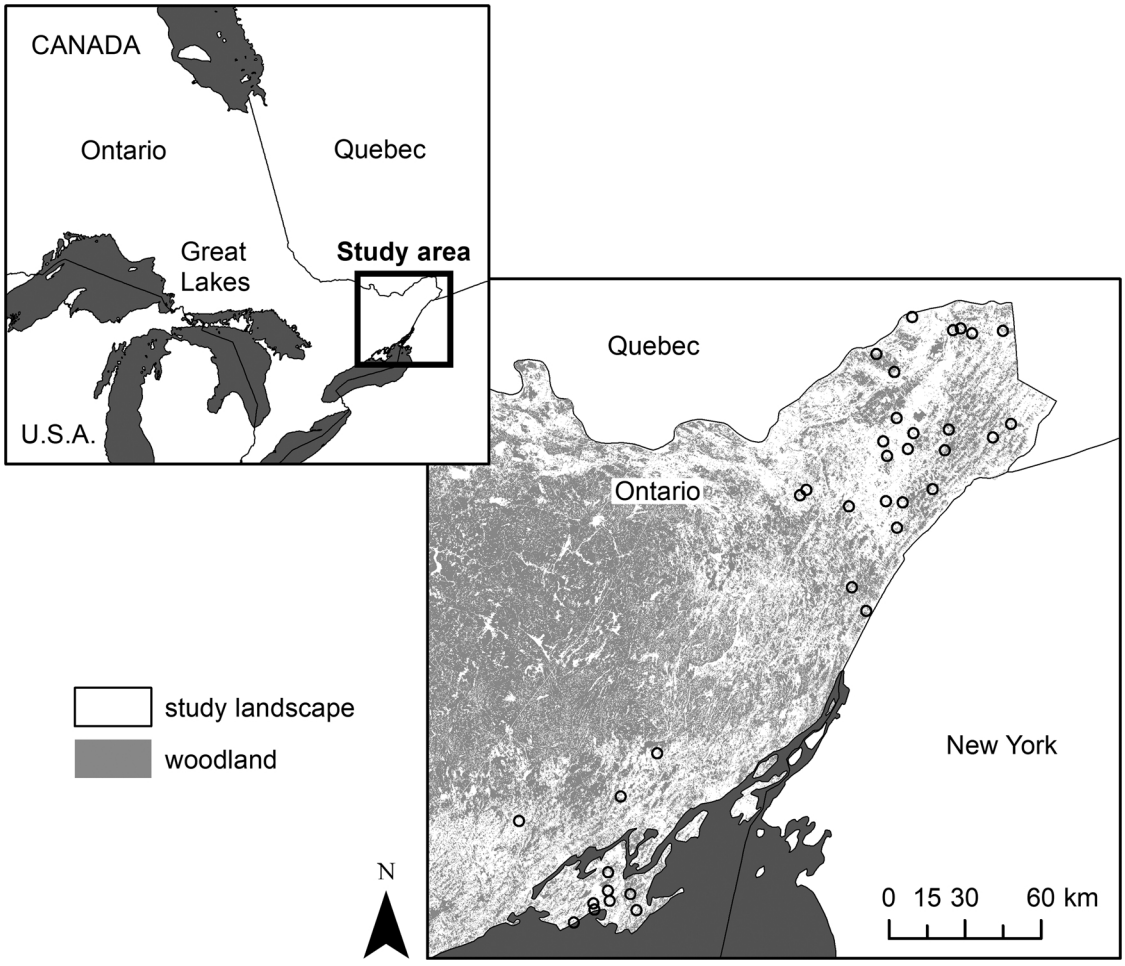

Fig. 1. Locations of the 36 study wetlands, each within a 2-km-wide surrounding landscape, in rural eastern Ontario, Canada.

whether it was contiguous with the wetland edge or not. Woodland cover was derived from existing GIS data (OMNR, 2013). We focused on woodland during site selection because (a) woodland is the dominant natural land cover type in the region, (b) previous studies have shown anuran species richness typically increases with woodland cover (e.g. Collins and Fahrig, 2017; Findlay et al., 2001; Herrmann et al., 2005; Houlahan and Findlay, 2003), and (c) it was the type of anuran habitat that we could distinguish most reliably in aerial photographs. We also selected wetlands to minimize any latitudinal or longitudinal gradients in the wooded buffer size or landscape-scale woodland cover, and ensured spatial independence of study wetlands by selecting wetlands that were at least 2 km apart. We controlled for wetland type by ensuring that all study wetlands were natural ponds or naturalized ponds (i.e. not used for agriculture for at least 5 years, or for quarrying for at least 20 years), consisting of open water with some emergent vegetation around the edges. We also controlled for wetland size by ensuring that all ponds were less than 0.5 ha in area, thus minimizing variation in size across landscapes. Additionally, we avoided selecting ponds adjacent to pasture, because cattle grazing activity and waste are associated with reduced amphibian richness and abundance (Schmutzer et al., 2008). Finally, all selected ponds were at least 150 m from major watercourses and 40 m from the nearest road. Potential study wetlands were located using GIS data (OMNR, 2011, 2010) and aerial photographs (Google, 2015; OMNR, 2009). Correlations between the wooded buffer size and landscape-scale woodland cover, and between each of these variables and the potentially confounding variables controlled for in our site selection (latitude, longitude, wetland size, distance to water, and distance to road) were weak: all |Spearman's correlation coefficients (ρ)| were ≤ 0.24 (Appendix A in Supplementary material).

2.3. Field data collection

We conducted four 10-minute anuran breeding call surveys per wetland, with one survey per month between April 14 and July 30, 2015. We generally sampled the more southern wetlands before the more northern wetlands within each month, because we expected that anurans would breed earlier at lower latitudes. However, we varied the combination of wetlands sampled on a given day (1–6 wetlands/day) and the time of day that each wetland was surveyed between months. All surveys were conducted at least 30 min after sunset, and before 01:30 the following morning. Surveys were only conducted on nights with temperatures > 0 °C in April and May, > 5 °C in June, and > 16 °C in July. Minimum acceptable temperatures were warmer in later months because later-breeding species require warmer temperatures for breeding than earlier-breeding species (Lannoo, 2005; Oseen and Wassersug, 2002). Surveys were only conducted when wind speed was ≤ 4 on the Beaufort scale and we avoided sampling during rain as much as possible (97% [139 / 144] of surveys were on rain-free nights). Eighty-nine percent of surveys (128 / 144 surveys) were conducted by two observers; otherwise observations were made by a single observer. In double-observer surveys, the difference in relative abundance estimates by the two observers was ≤ 4 individuals for each species in each survey. We note that when call frequencies for a given species were exceptionally high (≥ 30 calling individuals in 10 min) we recorded the relative abundance as 30, because we could not accurately estimate the number of calling individuals. This occurred in only 2% (3 / 144) of surveys.

We were unable to control for the amount of emergent vegetation across our sampled wetlands during site selection (see 2.2. Site

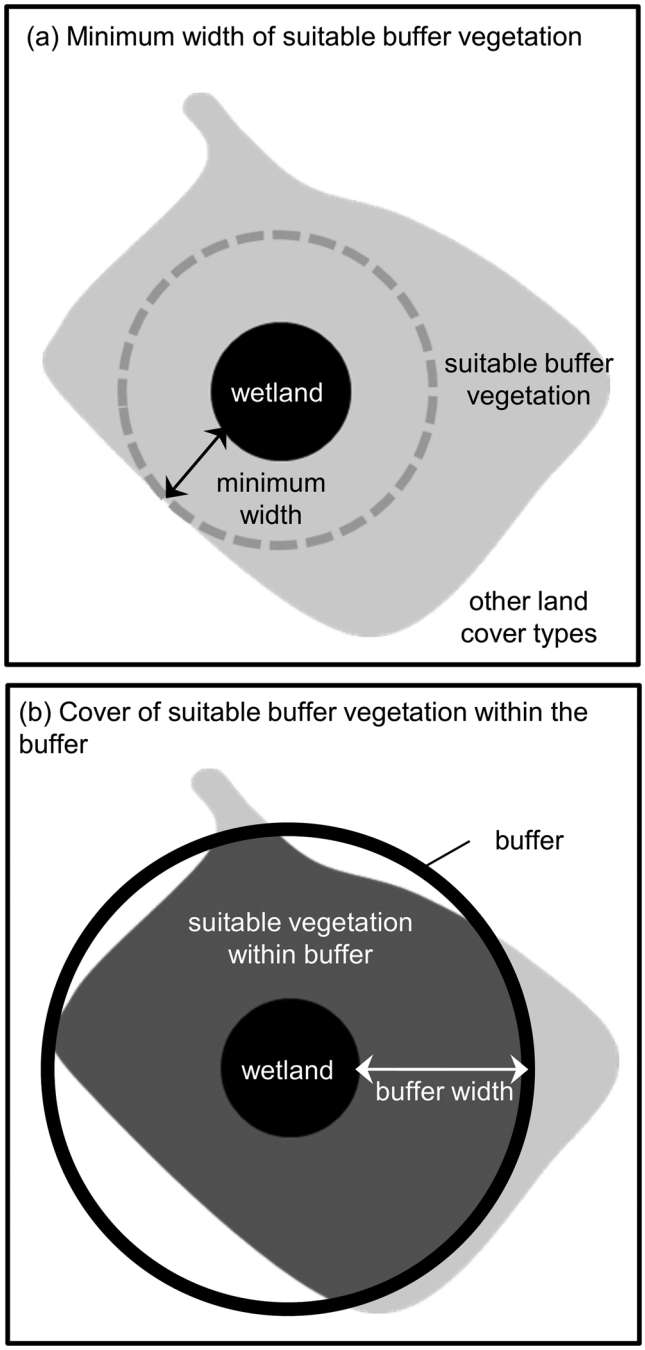

Fig. 2. Illustrations of the alternative ways we measured the size of the vegetated wetland buffer: (a) as the minimum width of suitable buffer vegetation (e.g. permanent vegetation, woodland) that is contiguous with the sampled wetland, or (b) as the area within 5, 16, 30, 50, 120, or 300 m around the wetland with suitable buffer vegetation contiguous with the wetland, divided by the total area within that radius.

selection, above). Therefore, M.E.S. revisited each sampled wetland in August 2018, to estimate the percent of each wetland covered by emergent vegetation, to the nearest 20%.

2.4. Wetland buffer measurements

It was not clear *a priori* which type(s) of land cover are most appropriate for a wetland buffer for anurans. Therefore, we considered seven possible types of suitable vegetation: permanent vegetation, permanent vegetation minus hay, natural vegetation, woodland, permanent open canopy (non-woodland), permanent open canopy minus hay, and scrub (Table 1). We included calculations of permanent vegetation and permanent open-canopy vegetation with and without hay, because hay—a perennial crop—is often rotated with annual row crops such as corn and soy in our study region, and thus might not represent a truly permanent land cover type. To calculate the seven types of suitable vegetation, land cover within 300 m of each wetland was classified into the following land cover classes using aerial photographs (Google, 2015; OMNR, 2009): woodland (all areas with continuous canopy), scrub (primarily grass, with scattered trees or shrubs), lawn, orchard, vineyard, pasture, hay, row crop (corn, soy, grains, or commercial vegetables), and non-vegetated (e.g. roads, quarries, or sand pits). Each of the seven possible suitable vegetation types included a subset of these land cover classes (Table 1).

We used seven different measures of wetland buffer size for each of the seven types of wetland buffer vegetation described above. First, we measured the minimum width of suitable buffer vegetation contiguous with the edge of the study wetland (C. Flemming, personal communication; Fig. 2a). The six remaining measures of buffer size were the proportion of the area within 5, 16, 30, 50, 120, or 300 m of the wetland containing buffer vegetation that was contiguous with the wetland (Fig. 2b). These widths were based on the different wetland buffer width guidelines that have been recommended for the conservation of Ontario wetland species (Coukell et al., 2004; Ontario Farm Environmental Coalition, 2004).

2.5. Measuring landscape-scale variables

We measured three landscape-scale variables: woodland cover, water cover, and road density. Each was measured at four landscape scales, with a landscape defined as the area within 0.5, 1, 1.5, or 2 km of the edge of the wetland. Woodland cover, water cover, and road density were derived from existing GIS data sets (OMAFRA, 2010; OMNR, 2014, 2013, 2012, 2011, 2010, 2002). Note that we did not include agricultural land cover as a landscape variable because it was highly correlated with woodland cover (e.g. $\rho = -0.9$ for the 1-km landscape scale).

2.6. Statistical analysis

2.6.1. Can wetland buffers increase anuran species richness and relative abundance in agricultural wetlands?

We used model selection to determine the level of support (AICc) for relationships between anuran species richness and each of our 49 wetland buffer measurements (7 buffer vegetation types × 7 ways of measuring the wetland buffer size), using generalized linear models with a Poisson distribution and log link. We also calculated the AICc for an intercept-only (null) model. We considered a wetland buffer effect to be supported if it (a) had a positive effect on anuran species richness, and (b) had an AICc value at least 2 points lower than that of the intercept-only model. Wetland buffer measures with a negative effect on species richness were excluded, as guidelines based on these would be counter-productive for anuran conservation. All wetland buffer measurements were standardized to a mean of zero and standard deviation of one prior to analysis. We tested for spatial autocorrelation in the residuals of each of the 49 candidate models, using a permutation approach (with 1000 permutations) to calculate the significance level for Global Moran's I. Residuals were considered spatially autocorrelated at $p < 0.05$.

We used model selection to test for relationships between relative anuran abundance and the 49 wetland buffer measurements and tested for spatial autocorrelation as described above, with the exception that here we used a generalized linear model with a negative binomial distribution and log link. We estimated relative anuran abundance at each study wetland as the total number of calling individuals across the four surveys.

Table 1
Land cover classes included in measurements of each of seven possible types of suitable vegetation for wetland buffers for anurans. ✓ = land cover class included.

Buffer vegetation type	Land cover class						
	Woodland	Scrub	Lawn	Orchard	Vineyard	Pasture	Hay
Permanent vegetation	✓	✓	✓	✓	✓	✓	✓
Permanent vegetation minus hay	✓	✓	✓	✓	✓	✓	
Natural vegetation	✓	✓					
Woodland	✓						
Permanent open canopy		✓	✓	✓	✓	✓	✓
Permanent open canopy minus hay		✓	✓	✓	✓	✓	
Scrub		✓					

We also used model selection to test for relationships between individual species' relative abundance/occurrence and the 49 wetland buffer measurements and tested for spatial autocorrelation, as described above. To ensure adequate sample sizes for modeling, we only tested for effects of wetland buffer sizes on abundance for the subset of species observed at > 25% of our study wetlands. For species found at 10–25% of wetlands we converted abundances to occurrence (presence-absence) data and modeled the relationships as described above but using generalized linear models with a binomial distribution and logit link. We did not model relationships for species found at < 10% of wetlands.

2.6.2. How strong are wetland buffer effects on anurans, relative to the effects of the landscape context?

First we estimated the scale of effect of each of the three landscape-scale variables (woodland cover, water cover, and road density) on each anuran response (anuran richness, relative anuran abundance, and the relative abundance/occurrence of individual species). To estimate the scale of effect of a given landscape variable on an anuran response we modeled the relationship between the response and landscape variable at each spatial scale (0.5, 1, 1.5, and 2 km). The scale of effect was the scale with the lowest AICc. We then used model averaging to estimate the strength of relationship between each anuran response and the 'best' measure of wetland buffer size—the measure with the lowest AICc from the subset of models where the effect on the anuran response was positive (see above)—and the three landscape-scale variables: woodland cover, water cover, and road density. Our candidate models included all possible combinations of these four predictor variables plus the percent cover of emergent vegetation, to control for its effects on anuran richness, relative anuran abundance, and the relative abundance/occurrence of individual species in wetlands. We also included the intercept-only (null) model in our candidate model set. We then estimated the strength of effect of each variable as the model-averaged slope of its relationship with the response variable. Relationships were modeled using generalized linear models with a Poisson distribution and log link for richness, negative binomial distribution and log link for relative abundance (of all anurans or of individual species), or a binomial distribution and logit link for occurrence. All predictors were standardized to a mean of zero and standard deviation of one prior to analysis. We considered a predictor's effect to be strongly supported if its 95% unconditional confidence interval did not cross zero. We tested for spatial autocorrelation in the residuals of the global model, as described above. Finally, we tested for collinearity by calculating ρ for all pairs of our five predictor variables. We considered variables to be strongly correlated at $|\rho| > 0.70$.

All statistical tests were performed in R Version 3.4.0 (R Core Team, 2017), using the 'MASS' (Venables and Ripley, 2002),'MuMIn' (Barton, 2016), and 'spdep' (Bivand and Piras, 2015; Bivand et al., 2013) packages. Data used in these analyses are available through Mendeley Data (Sawatzky et al., 2018).

3. Results

We found on average four anuran species per wetland (range 1–6), with a total of 10 species observed across the study wetlands. Five of the 10 species were observed at > 25% of wetlands: green frog (*Lithobates clamitans*) at 92%, spring peeper (*Pseudacris crucifer*) at 83%, common gray treefrog (*Dryophytes versicolor*) at 64%, northern leopard frog (*Lithobates pipiens*) at 61%, and wood frog (*Lithobates sylvaticus*) at 33% of wetlands. American toad (*Anaxyrus americanus*) was observed at 25% of wetlands. The remaining four species were observed at less than 10% of wetlands: American bullfrog (*Lithobates catesbeianus*) at 8%, western chorus frog (*Pseudacris triseriata*) at 6%, mink frog (*Lithobates septentrionalis*) at 3%, and Cope's gray treefrog (*Dryophytes chrysoscelis*) at 3%. There were on average 34 calling anuran individuals per wetland (range 1–85). The average percent cover of emergent vegetation, estimated to the nearest 20% in each wetland, was 26% (range 0–80%).

3.1. Can wetland buffers increase anuran species richness and relative abundance in agricultural wetlands?

We found little to no support for positive effects of wetland buffer size on anurans. All models with estimated positive effects of wetland buffers on anuran richness or relative anuran abundance performed similarly to (within 2 AICc), or worse than, the intercept-only model (Fig. 3a,b). Positive effects of wetland buffer size on the relative abundance/occurrence of individual species were only supported for two of the six species with enough data to model individually. American toads were more likely to occur in wetlands with more contiguous open-canopy cover (excluding hay) within a 50 m radius (Fig. 3c), and green frogs were more abundant in wetlands with more contiguous open-canopy cover (whether hay cover was included or excluded) within a 5 m radius (Fig. 3e).

Surprisingly, the strongest effects of vegetated wetland buffers were negative for most of our anuran response variables (6 / 8 responses; Fig. 3). The most supported model of anuran richness predicted fewer species in wetlands with a wider woodland buffer than in wetlands with a narrower woodland buffer (Fig. 3a). Similarly, the most supported models of relative anuran abundance, as well as the relative abundances of green frogs and northern leopard frogs, predicted fewer frogs in wetlands with a wider woodland buffer (Fig. 3b,e,f). The most supported model of wood frog relative abundance predicted fewer frogs in wetlands with more permanent vegetation within a 300 m radius (Fig. 3h).

Model residuals were not spatially autocorrelated (all $p > 0.05$), with one exception (Appendix B in Supplementary material). Residuals from the model of the relationship between species richness and proportional cover of permanent open-canopy vegetation minus hay within a 300 m buffer showed significant positive spatial autocorrelation ($I = 0.33$, $p = 0.04$). This means that spatial autocorrelation was detected in only 1 / 392 of the models used to determine whether wetland buffers increase anuran species responses (anuran richness, relative anuran abundance, or the relative abundance/occurrence of individual

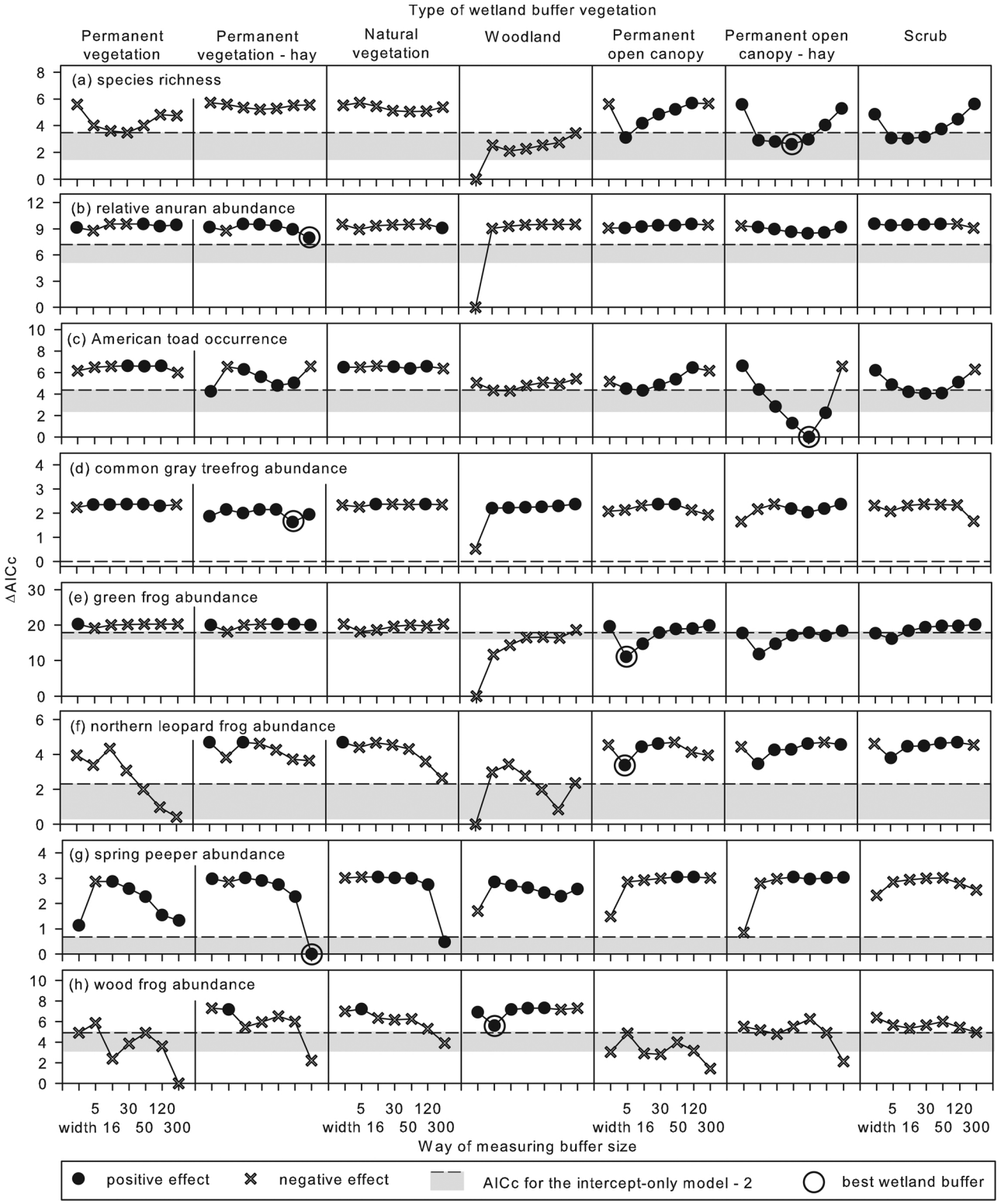

Fig. 3. Level of support for relationships between each of eight anuran response variables and each of 49 different measurements of the vegetated wetland buffer size, where relationships were modeled using generalized linear models with a Poisson distribution and log link for richness, a negative binomial distribution and log link for relative abundance, or a binomial distribution and logit link for occurrence. We measured the wetland buffer size as the minimum width of suitable buffer vegetation contiguous with the edge of the study wetland or the proportion of the area within 5, 16, 30, 50, 120, or 300 m of the wetland containing buffer vegetation that was contiguous with the wetland, for each of seven different types of buffer vegetation (see Table 1). Positive effect = an increase in anuran richness, relative anuran abundance, or the relative abundance/occurrence of individual species with increasing vegetation width or proportional vegetation cover. Negative effect = a decrease in anuran richness, relative anuran abundance, or the relative abundance/occurrence of individual species with increasing vegetation width or proportional vegetation cover. Best wetland buffer = the wetland buffer measurement with the lowest AICc from the subset of models where the effect on the anuran response was positive.

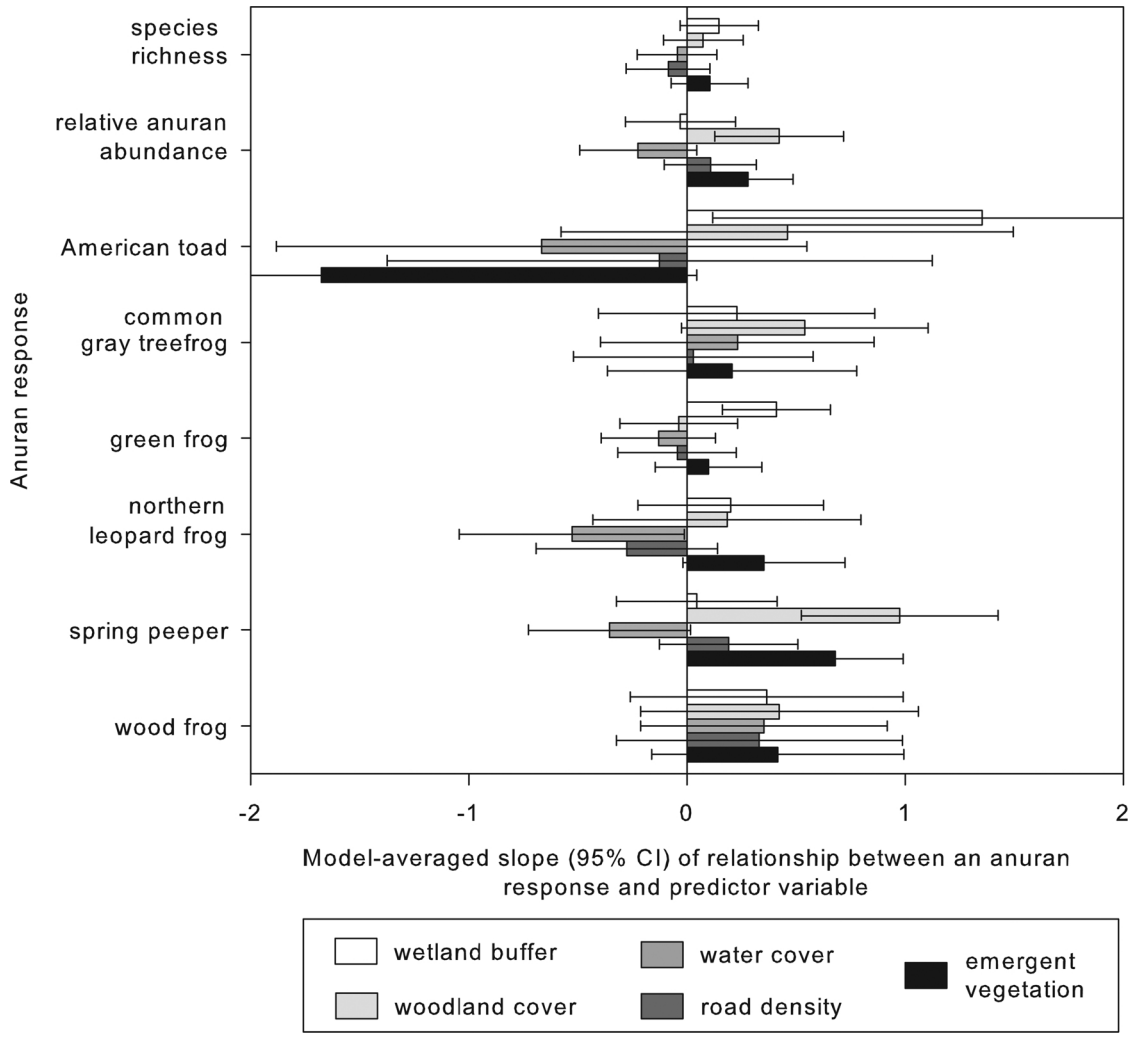

Fig. 4. Model-averaged slopes (95% unconditional confidence interval) of the relationships between an anuran response and the best wetland buffer, three landscape-scale variables (each measured at its scale of effect; see Appendix C in Supplementary material), and percent cover of emergent vegetation in the study wetland. The best wetland buffer was the one with the lowest AICc from the subset of models where the effect on the anuran response was positive. Relationships were modeled using generalized linear models with a Poisson distribution and log link for richness, a negative binomial distribution and log link for relative abundance, or a binomial distribution and logit link for occurrence. Slopes were averaged for the entire candidate model set, which included all possible combinations of the five predictor variables plus the intercept-only (null) model.

species) in agricultural wetlands (8 response variables × 49 wetland buffer measurements). Given the large number of tests conducted, the probability of finding at least one Type II error approached 100% ($1 - [1 - 0.05]^{392} \times 100$); thus we did not correct models for spatial autocorrelation.

3.2. How strong are wetland buffer effects on anurans, relative to the effects of the landscape context?

For species richness, the model-averaged effect of the best wetland buffer was somewhat larger than the effects of the landscape-scale variables (woodland cover, water cover, and road density). Specifically, the effect of wetland buffer size was 1.7 times larger than the strongest landscape-scale effect (road density; Fig. 4). However, neither wetland buffer size nor landscape-scale variables had strongly-supported effects on species richness, i.e. the 95% confidence interval for each predictor crossed zero (Fig. 4).

In contrast, for relative anuran abundance the effects of woodland cover, water cover, and road density were 14.2 times, 7.5 times, and 3.6 times larger than the effect of the wetland buffer, respectively (Fig. 4). Furthermore, while effects of woodland cover on relative anuran abundance were strongly supported (i.e. its 95% confidence interval did not cross zero), the effect of the wetland buffer was not. Thus our models predict that relative anuran abundance primarily increases with the amount of woodland within 1 km of the pond (Appendix C in Supplementary material).

Although the landscape context was much more important than a vegetated wetland buffer for relative anuran abundance, the relative importance of the wetland buffer versus landscape context for individual species' abundance/occurrence varied. The effect of landscape context was more important than the effect of the wetland buffer for four of the six species with enough data to model individual species' abundance/occurrence. Specifically, we found that the effects of the strongest landscape-scale variable were 21.5, 2.6, 2.4, and 1.2 times larger than the effects of wetland buffer size for spring peepers (woodland cover), northern leopard frogs (water cover), common gray treefrogs (woodland cover), and wood frogs (woodland cover), respectively (Fig. 4). The effect of wetland buffer size was larger than the effects of landscape-scale variables for the other two species, with effects of buffer size that were 3.1 and 2.0 times larger than the strongest landscape-scale effect for green frogs and American toads, respectively (Fig. 4).

Anuran richness, relative anuran abundance, and the abundance of individual species generally increased with the percent cover of emergent vegetation in sampled wetlands (Fig. 4). Only American toads were less likely to occur in wetlands with more emergent vegetation; however, this effect was not supported by multi-model inference (the 95% confidence interval crossed zero).

We did not detect significant spatial autocorrelation in model residuals for any of the above models (all $p > 0.09$; Appendix B in Supplementary material) and collinearity among our five predictor variables was generally low (Appendix D in Supplementary material). Only woodland cover and water cover within 1 km were strongly correlated ($\rho = 0.72$). These variables were only included at the 1 km-scale in analyses of the relative effects of wetland buffers versus landscape-scale variables on relative anuran abundance and the relative abundance of spring peepers.

4. Discussion

Our results do not support reliance on wetland buffers as a conservation strategy for amphibians in agriculture-dominated landscapes. We did not find support for positive effects of wetland buffer size on anuran richness or relative anuran abundance for any of the tested buffer widths or buffer vegetation types. We similarly were unable to find support for positive effects of wetland buffers on the relative abundances of common gray treefrogs, northern leopard frogs, spring peepers, or wood frogs. Positive effects of wetland buffers on individual species' abundance/occurrence were only supported for two species: American toads and green frogs were both more likely to occur in wetlands surrounded by more contiguous open-canopy cover (within a 50 m and 5 m radius, respectively). These positive effects of open-canopy cover are generally consistent with known habitat use for these species: American toads typically prefer grassland habitat as adults (Green, 2005) and green frogs use open-canopy, terrestrial habitat close to ponds (Birchfield and Deters, 2005; Pauley, 2005). Nevertheless, the majority of anurans in our study did not respond positively to wetland buffer size.

We suggest that wetland buffers that protect terrestrial habitat for amphibians within 300 m—the maximum government-recommended wetland buffer size in Ontario—have limited benefits for many anurans because they are too narrow to encompass the landscape context anurans experience. Anurans can move much farther than 300 m during dispersal (Baldwin et al., 2006; Forester et al., 2006; Semlitsch, 2008; Semlitsch and Bodie, 2003). Some anurans may also be more dependent on the availability of terrestrial habitat in the surrounding landscape than the availability of foraging habitat directly adjacent to the breeding pond. Indeed, wood frog, chorus frog, spring peeper, common gray treefrog, and Cope's gray tree frog can all overwinter in terrestrial habitat (Costanzo et al., 1992; Edwards et al., 2000; Layne and Rice, 2003; Layne and Jones, 2001; Swanson et al., 1996). Additionally, the landscape context can impact aspects of water quality within breeding wetlands at scales much larger than 300 m (Houlahan and Findlay, 2004).

Consistent with this, the landscape context had stronger effects on relative anuran abundance than a vegetated wetland buffer in our study. Woodland cover was 14.2 times more important, water cover 7.5 times more important, and road density 3.6 times more important than the wetland buffer size. We suggest that this result is not an artefact of our study design, for several reasons. First, the effect of wetland buffer size on relative anuran abundance was not likely to be obscured by collinearity between measurements of buffer size and landscape-scale environmental conditions because these measures were only weakly correlated ($|\rho| = 0.01$–0.56; Appendix D in Supplementary material). Furthermore, Smith et al. (2009) showed that model-averaged coefficients generally produce unbiased estimates of effect sizes even when variables are collinear. Second, it is unlikely that stronger effects of landscape context versus the wetland buffer occur because the data used to estimate the wetland buffer size was of lower quality than the data used to estimate landscape-scale variables. In fact, the data used to estimate wetland buffer sizes was of higher quality than the data used to estimate landscape-scale variables. Our measurements of wetland buffers were based on fine-scale classification of land cover from aerial photos and intensive on-the-ground manual examination by M.E.S., whereas the data used to estimate landscape-scale variables were based on coarser-scale GIS data sets combining data from various sources (OMAFRA, 2010; OMNR, 2014, 2013, 2012, 2011, 2010,). Finally, the stronger effect of landscape-scale variables than wetland buffer size was not due to higher variation across sites in the landscape-scale variables than in the wetland buffer size (see Eigenbrod et al., 2011). The range of variation in standardized wetland buffer sizes across sites was 0.77–1.13 times the range of variation in standardized landscape-scale variables across sites. Thus we conclude that the most likely explanation for the stronger effects of landscape context than the wetland buffer on relative anuran abundance is that anurans are most affected by the landscape context of a wetland at scales much larger than even the maximum tested buffer size of 300 m.

Apart from the difference in spatial extent, the other major difference between our measurements of the wetland buffer size and landscape-scale variables is that we considered only the terrestrial habitat that was contiguous with the wetland when measuring buffer size, while the landscape-scale variables included the whole area of the terrestrial habitat within the landscape extent, regardless of whether it was contiguous with the wetland. That the wetland buffer was much less important than the landscape-scale variables suggests that contiguity of terrestrial habitat with the wetland is not important for relative anuran abundance. In other words, it is the total amount of habitat within a given distance that matters, not its spatial configuration (Fahrig, 2017, 2003).

Of the three landscape-scale variables, woodland cover had the strongest effect on the relative abundance of anurans in agricultural wetlands. Similarly, woodland cover had a consistently positive effect on individual species' relative abundance/occurrence (Fig. 4), with the exception of green frogs. This strong, positive effect of woodland cover is consistent with previous studies in our region (Collins and Fahrig, 2017; Koumaris and Fahrig, 2016). This likely occurs because woodland provides suitable non-breeding habitat for many of our study species (as reviewed in Koumaris and Fahrig, 2016).

Given the positive effects of woodland amount at a landscape scale, we were surprised to find that effects of woodland on anurans at the buffer scale were often negative. The most supported model of anuran richness predicted fewer species in wetlands with a wider woodland buffer than in wetlands with a narrower woodland buffer. Similarly, relative anuran abundance, as well as the abundances of green frogs and northern leopard frogs, was lower in wetlands with a wider woodland buffer. We speculate that some anurans may respond negatively to the amount of woodland in the wetland buffer because (a) wetlands are more shaded when there are more trees in the surrounding buffer and (b) shading has negative effects on some species' growth rates and/or survivorship. For example, previous studies have found that growth rates and/or survivorship of American toads, northern leopard frogs, spring peepers, and wood frogs are lower in wetlands with more shade (Skelly et al., 2002; Werner and Glennemeier, 1999). Additionally, wetlands with more woodland in the buffer are likely to have less suitable habitat for species preferring open-canopy land cover types, such as the green frog.

We also did not expect to find that American toads, green frogs, northern leopard frogs, and spring peepers were less likely to occur or were less abundant in wetlands surrounded by more water cover, although we note that this effect was only strongly supported for northern leopard frogs. This contrasts with previous studies, which have shown anurans are more likely to occur in landscapes with more wetland cover, presumably because larger amounts of aquatic habitat in the landscape foster larger anuran metapopulations (Jeliazkov et al., 2014;

Knutson et al., 1999; Pope et al., 2000). We speculate that farmland ponds are less suitable breeding habitat than are more natural or secluded wetlands; thus when multiple natural wetlands are available in the surrounding landscape, anurans may select these wetlands instead of farmland ponds for breeding. However, future research is needed to evaluate this hypothesis.

4.1. Conservation implications

Our study suggests that wetland buffers that protect terrestrial habitat for anurans within 300 m—the maximum government-recommended wetland buffer size in Ontario—are likely to have limited conservation benefits in agricultural landscapes, at least when the objective is the conservation of anuran richness and/or abundance. Instead, our study suggests that anurans in agricultural landscapes are more affected by the landscape context than by land cover contiguous with the wetland. In particular, we recommend that terrestrial conservation initiatives for anurans in farmland in our study region should focus on maintaining or increasing the amount of woodland cover at the landscape scale, regardless of whether that woodland is contiguous with a wetland or not.

This recommendation is broadly consistent with the "land sparing" approach to conservation in agricultural areas, i.e. the setting-aside of areas of natural land cover for conservation purposes. However, the debate over the efficacy of land sparing for conservation versus the opposite strategy of land sharing—which involves conservation of biodiversity in farmland via adoption of wildlife-friendly practices—typically hinges on a tradeoff between farmland biodiversity and crop yields (e.g. Green et al., 2005; Hodgson et al., 2010; Phalan et al., 2011). Land sharing allows for better outcomes for wildlife within the farmed portion of the landscape but lower yields; thus a larger total area is needed for crop production. In contrast, land sparing reduces the total area needed for crop production via high-intensity, yield-maximizing farming practices that have poorer outcomes for wildlife within the farmed portion of the landscape. Determining whether landscape-scale conservation of forest produces better outcomes for anurans than wildlife-friendly farming practices (e.g. reduced pesticide and fertilizer use) for a given agricultural yield is beyond the scope of this study. Thus future research is required to determine whether increasing agricultural intensity to "spare" forests (or other natural land covers) produces better conservation outcomes for anurans than adoption of wildlife-friendly farming practices.

Although wetland buffers do not appear to have strong effects on overall anuran richness or abundance, we stress that this does not negate the potential benefits of wetland buffers for conservation of individual anuran species or other taxa, or benefits of buffers for water quality. For example, we found strong, positive effects of wetland buffers with more permanent open-canopy cover for both American toads and green frogs. Additionally, previous study has found that there can be positive effects of wetland buffers on other taxa; for example, Raebel et al. (2012) found more odonate species in agricultural wetlands with wetland buffers than in wetlands without buffers. Large enough wetland buffers can also effectively reduce or mitigate the effects of pesticide and fertilizer use on water quality (e.g. Mayer et al., 2007; Sawatzky, 2016). Nevertheless, our study suggests that wetland buffers do not effectively conserve anuran abundance and diversity in agricultural wetlands.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at https://doi.org/10.1016/j.agee.2018.09.021.

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