

Relative effects of landscape-scale wetland amount and landscape matrix quality on wetland vertebrates: a meta-analysis

PAULINE E. QUESNELLE,^{1,3} KATHRYN E. LINDSAY,^{1,2} AND LENORE FAHRIG¹

¹*Geomatics and Landscape Ecology Research Laboratory, Ottawa-Carleton Institute of Biology, Carleton University, Ottawa, Ontario K1S5B6 Canada*

²*Wildlife and Landscape Science, National Wildlife Research Centre, Environment Canada, Ottawa, Ontario K1A0H3 Canada*

Abstract. Conservation management of wetland-dependent species generally focuses on preserving or increasing wetland habitat. However, the quality of the landscape matrix (the intervening non-wetland portion of the landscape) has been shown to be more important than wetland availability for some wetland-dependent species. We used meta-analysis to compare the effects of wetland amount (measured as the area of wetland habitat in a landscape) and matrix quality (measured as the area of forest cover in the same landscape) on the population abundance of wetland-dependent vertebrates. We combined data across 63 studies conducted in forested ecoregions worldwide and extracted 330 population responses for 155 species, at the spatial scale that best predicted the effects of wetland amount and forest amount for each response. In addition, to ensure that our results were not biased by the scale selected, we assessed whether the relative effects of wetland and forest amount were scale dependent. We found that the amount of wetland in a landscape had a larger effect than the amount of forest on the abundance of mammals and birds whereas, surprisingly, for amphibians the amount of forest in a landscape was more important than the amount of wetland. For reptiles, both wetland amount and forest amount showed only weak effects on abundance. These results were not scale dependent, i.e., they were consistent across spatial scales. Our results suggest that the population distribution of wetland-dependent amphibians is more strongly related to landscape matrix quality than to wetland availability in a landscape, likely due to their requirement for access to terrestrial resources. We conclude that conservation policies for wetland biodiversity that focus only on wetland habitat will be ineffective in conserving many of these species. In addition, population viability analyses based only on wetland amount may overestimate the capacity of a landscape to support populations of wetland-dependent species.

Key words: *amphibians; aquatic mammals; fragmentation; habitat loss; landscape scale; marsh birds; matrix quality; meta-analysis; relative effects; reptiles; wetland-dependent species; wetlands.*

INTRODUCTION

Wetland-dependent species are undergoing some of the largest wildlife population declines worldwide, primarily due to habitat loss (Millennium Ecosystem Assessment 2005). Although it is widely recognized that many wetland-dependent species depend on more habitat types than just wetlands (Semlitsch and Bodie 2003), conservation management of these species generally focuses on preserving or increasing wetland habitat in a region. This focus is reinforced not only by the simple fact that we label these organisms “wetland-dependent,” but also by the patchy nature of wetland habitat, which has led to the common assumption that many wetland-dependent species function as metapopulations (Gibbs 2000, Marsh and Trenham 2001, Vermaat et al. 2008). Thus, the most common policies used to protect wetland-dependent species are wetland

regulations that preserve the wetlands themselves and, in some cases, small terrestrial buffers surrounding the wetlands (Haig et al. 1998, Semlitsch and Bodie 2003, Bauer et al. 2010). For example, worldwide establishment of wetland reserves (e.g., Ramsar Convention), international strategies to identify and protect key wetlands (e.g., North American Waterfowl Management Plan), and regional “no net loss” wetland policies (e.g., U.S. National Wetlands Mitigation Action Plan) primarily focus on preserving individual wetlands and groups of wetlands, or maintaining some total amount of wetland in a landscape, to conserve wetland biodiversity. Moreover, large-scale wetland restoration and creation aimed at increasing wetland amount in a landscape is common practice for wetland-dependent species recovery plans (e.g., Gilbert et al. 2005) and to increase overall wetland biodiversity (Moreno-Mateos and Comín 2010).

However, for some wetland-dependent species, the quality of the surrounding landscape matrix (the intervening non-wetland portion of the landscape) can be more important than the amount of wetland in a

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³ E-mail: pauline.quesnelle@glel.carleton.ca

landscape. For example, the amount of cropland in a landscape was found to have a larger effect than wetland amount on wetland breeding bird occurrence in the Prairie Pothole Region of South Dakota (Naugle et al. 1999) and agricultural landscapes of northeastern Spain (Cardador et al. 2011). Similarly, the amount of forest in a landscape was found to be relatively more important than the amount or spatial distribution of wetlands in a landscape for the abundance of several wetland-breeding amphibians (Houlahan and Findlay 2003, Rubbo and Kiesecker 2005, Denoël and Ficetola 2008), as well as the occurrence of two freshwater turtle species and one water snake species (Attum et al. 2007, Quesnelle et al. 2013). Moreover, roads and/or urban development have been found to be better predictors of the abundance and distribution of several amphibians (Vos and Chardon 1998, Pillsbury and Miller 2008, Veysey et al. 2011) and freshwater turtles (Rizkalla and Swihart 2006) than the amount of wetland in a landscape. If other landscape variables are often more important than wetland amount for wetland-dependent species, then conservation strategies that focus solely on preserving and/or increasing wetlands in a given landscape are likely to be ineffective at protecting these declining species.

In this study, we conducted a meta-analysis to determine whether, and for what species groups, the focus on wetland conservation is likely to fail to conserve populations of wetland-dependent species. We note that this issue has been raised in several papers, for several individual species or groups of wetland-dependent species (Semlitsch and Bodie 2003, Roe et al. 2006, Roe and Georges 2007), but has never been generally assessed across a range of wetland-dependent vertebrate taxa using quantitative methods. We compared the relative effects of wetland amount and matrix quality by combining the information in all available studies of wetland-dependent species using meta-analysis. We measured wetland amount as the area of wetland habitat in a landscape. We measured matrix quality as the area of forest cover in the same landscape (here “forest amount”), where a landscape with more forest is assumed to represent a landscape with higher matrix quality. We had two reasons for making this assumption. First, forest amount in a landscape generally has a positive influence on wetland biodiversity and is typically negatively correlated with indicators of low matrix quality, such as road density in forested ecoregions (Findlay and Houlahan 1997). Second, the meta-analytic approach required us to independently estimate matrix quality for multiple studies across the globe, and forest is a land cover type that can be confidently measured from classified satellite imagery data sets. We quantitatively synthesized the results of 63 studies conducted in forested ecoregions across five continents that quantified the relationship between wetland-dependent animal abundance and wetland amount in a landscape (Fig. 1). From these we obtained 330 population responses to wetland amount for 155

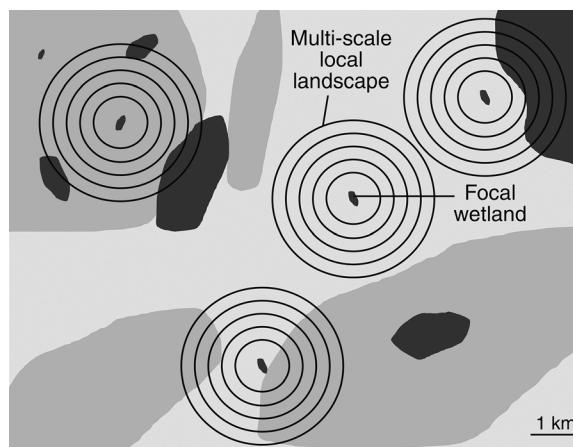


FIG. 1. Example of the sampling design of a landscape-scale study included in the meta-analysis. A species response (occurrence, abundance, or density) is sampled at a set of focal wetlands within a study area. The study area is composed (for simplicity) of three land cover types: wetland (dark gray), forest (medium gray), and field (light gray). Wetland amount (area of wetland cover) and forest amount (area of forest cover) are measured within nested local landscapes at multiple spatial scales surrounding each sampled wetland. The scale of effect is the spatial scale where the strength of the relationship between species response and wetland amount (or forest amount) is the greatest.

species including mammals, birds, amphibians, and reptiles. We also obtained information on forest cover around each wetland in each of these studies, and then compared the strength of the relationship between species abundance and wetland amount to the strength of the relationship between abundance and forest amount.

METHODS

Study selection criteria

During our literature review and subsequent effect size extraction, we recorded the number of articles identified and the number of studies included and excluded based on our inclusion criteria according to the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) Statement, and we also recorded the number of studies involved at each step of the meta-analysis (Fig. 2). The studies included in this meta-analysis are a subset of a larger review of 90 studies that quantified the relationship between the amount of wetland in a landscape and population abundance of at least one wetland-dependent species (Quesnelle et al. 2014; Fig. 2, steps 1–3). Wetland amount was measured as the percentage of wetland area in a landscape (i.e., spatial scale) or wetland connectivity (or isolation). The current analysis includes all of the studies in the previous analysis for which we could obtain an effect size representing the relationship between population abundance and forest cover in the surrounding landscape (Fig. 2, step 4). In other words,

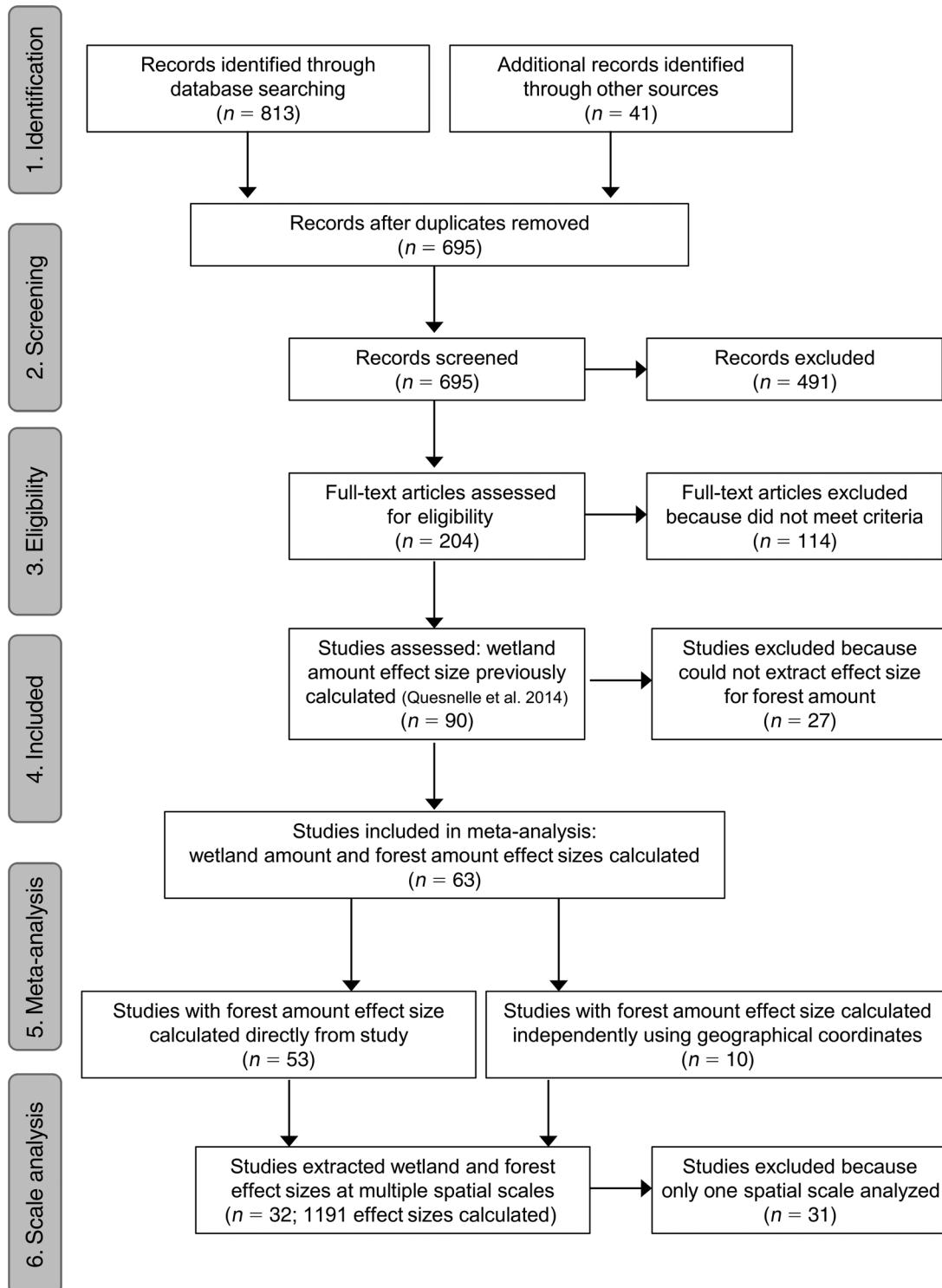


FIG. 2. Modified PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analysis) flow diagram indicating the number of studies considered at each step (identified in vertical boxes on left) of the literature search and meta-analysis.

we limited the set of studies to those that measured forest amount (or for which we could obtain forest amount) as the percentage of forest area in a landscape or the distance to the nearest forest (nearest neighbor),

depending on how wetland amount was measured (as area or distance). Wetland amount and forest amount data also had to be measured or measurable at the same spatial scale(s). We also limited our studies to ecoregions

where the terrestrial cover was predominately forested, which removed studies from ecoregions with naturally low forest cover, such as prairie/scrubland ecoregions.

Studies were found using a comprehensive search in the Web of Science and ProQuest dissertation and theses databases on 1 December 2011 using the following keyword string: (wetland* OR marsh* OR swamp* OR pond*) AND (amount OR area OR isolat* OR fragmentation) AND (amphib* OR turtle* OR reptile* OR mammal* OR bird*) AND (abundance* OR occurrence* OR occup* OR distribution) AND (species OR population*) AND (landscape*). We limited our analyses to empirical studies that were conducted in wetlands, including natural wetlands (e.g., pond, marsh) and artificially created wetlands (e.g., stormwater basins, rice fields). For all studies, we assumed that the authors accurately selected wetland types as habitat for each species. Note that different wetland types (e.g., pond, swamp) and forest types (e.g., deciduous, mixed) were measured within and across studies included in the meta-analysis. We were unable to separate out different wetland or forest types for further analysis because we did not have data of sufficient thematic resolution at the landscape scale. We used a broad definition of “population abundance” to include population size (or relative abundance), population density (or relative density), and species occupancy (as an index of low vs. high abundance). We defined “wetland-dependent species” as any vertebrate (mammal, bird, reptile, or amphibian) that uses wetlands as primary habitat for at least one part of its life cycle. We included species complexes that were fertile hybrids (e.g., *Pelophylax esculentus*) or two species that could not be distinguished (e.g., larval stages of *Ambystoma* spp.) as one species in the meta-analysis. When a study combined abundance or occurrence data across species, such that values for individual species could not be extracted, we contacted the authors for raw data or excluded the study. When a study combined wetland amount and other landscape variables into one landscape index (e.g., principal component), such that responses to wetland amount could not be extracted, we contacted the authors for raw data or excluded the study.

Effect size extraction

We had two effect sizes (ES) in our meta-analysis: wetland ES, representing the quantitative relationship between population abundance of a given wetland species and the amount of wetland in a landscape, and forest ES, representing the quantitative relationship between population abundance for the same wetland species and the amount of forest in a landscape. To extract an effect size from each study, we first searched the paper for a test statistic for the effect of wetland amount and forest amount on animal abundance. If a test statistic was not available, we looked for summary statistics (e.g., mean and variance) and corresponding sample size that could be converted into an effect size.

When these values were not reported, we calculated them using raw data if they were provided in the paper, if we could obtain them from the authors, or if we could extract them from figures using GetData Graph Digitizer 2.25 (Fedorov 2012; software *available online*).⁴

When a study did not measure forest amount in a landscape, or when forest was not measured at the same spatial scale(s) as wetland amount, we contacted authors to obtain raw abundance data and associated spatial coordinates (with datum and projection information) of each sample landscape so that we could independently estimate the relationship between abundance and forest amount. We used the coordinates to measure the area of surrounding forest cover in each sample landscape using classified satellite imagery data sets (Fig. 2, step 5). For studies within the United States, we used the National Land Cover Data (Fry et al. 2011), a 30-m resolution classified land cover data set based on Landsat Thematic Mapper (TM) satellite imagery from 2006. For studies outside of the United States, we used the Landsat Tree Cover, a 30-m resolution continuous tree cover data set based on Landsat-5 TM and/or Landsat-7 Enhanced Thematic Mapper Plus (ETM+) from 2000 and 2005 (Sexton et al. 2013). The Tree Cover data set estimates the percentage of horizontal ground in each pixel covered by woody vegetation greater than 5 m in height (i.e., tree cover) across the globe. We classified pixels with >50% tree cover as forest. We then measured forest amount in each of the study landscapes at the same spatial scale(s) that the study measured wetland amount using ArcGIS 10.

When a single study reported results for more than one species, we entered each species' effect size as an independent estimate. We did not calculate an effect size for species that occurred in $\leq 10\%$ of sampled landscapes or locations in a particular study. When a single study presented more than one effect size for a given species such that different effect sizes represented responses of the same species to different wetland types and/or forest types, we averaged these estimates across wetland types and/or forest types to extract a single effect size for that species, to avoid nonindependence (three studies). When a single study presented data in multiple years using the same study design, we averaged estimates across years for continuous data or tallied the numbers of years present for occupancy data. When studies measured effects of wetland amount and forest amount at multiple spatial scales, we calculated an effect size for each variable at each scale. We then selected the largest estimate across scales measured for each of wetland ES and forest ES, on the assumption that this scale was closest to the scale at which each landscape variable best predicts the species' response (i.e., scale of effect, sensu Jackson and Fahrig 2012).

⁴ getdata-graph-digitizer.com

TABLE 1. Study design moderator variables included in the meta-analysis.

Moderator variable and categories	Description
Study type	
Amount-based	Wetland amount was measured as percentage wetland area in a landscape or buffer (area-based buffers).
Configuration-based	Wetland amount was measured as the number of wetland patches in a landscape, or using wetland isolation (nearest-neighbor distances) or connectivity (incidence function model) metrics.
Sampling effort	
Area-dependent	Sampling effort increased in proportion to the sampled wetland area.
Area-independent	Sampling effort was consistent across sampled wetlands.
Unknown	Relationship between sampling effort and sampled wetland area was unknown.
Patch area	
Included	Sampled wetland area was included in the calculation of wetland amount in the landscape.
Not included	Sampled wetland area was not included in the calculation of wetland amount in the landscape.
Response type	
Abundance	Population response was measured as relative abundance.
Density	Population response was measured as relative density.
Occupancy	Population response was measured as occupancy, to index low vs. high abundance.
Correlation	
Continuous	Correlation between wetland amount and forest amount in a study.

Study design moderators

We identified five study design moderators to test if differences in study design influenced the magnitude and direction of the effect sizes, and to statistically control for such effects in remaining analyses (Table 1). First, the wetland ES or forest ES might vary depending on how wetland or forest amount in a landscape was measured. We combined several measures of wetland amount, including simple area-based measures and nearest-neighbor distances, as well as more complex connectivity indexes based on the incidence function model, because these measures have been shown to be highly correlated and have similar performance in predicting ecological responses (Moilanen and Nieminen 2002, Bender et al. 2003, Tischendorf et al. 2003, Prugh 2009, Ranius et al. 2010, Thornton et al. 2011, Martin and Fahrig 2012). These comparative studies also suggest that measures with more information about the amount of (occupied) habitat in the landscape are better predictors, and therefore we expected a priori that studies using such measures would have larger effect sizes. We distinguished two study types, (1) amount-based studies, where wetland amount was calculated as the percentage of wetland area in a landscape or buffer surrounding the sampled wetland patch, or (2) configuration-based studies, where the configuration of wetland habitat was included in the calculation of the measure, such as the number of wetland patches in a landscape, nearest-neighbor distances, wetland proximity, or wetland connectivity. For all study types, we applied the convention that each effect size extracted from a study should represent the population response of a species to increasing wetland amount (or forest amount) in a landscape. However, for nearest-neighbor

studies, a negative effect of increasing distance indicates that a species responded positively to closer wetlands (or forests), or equivalently, greater wetland (or forest) amount within the surrounding landscape. Therefore, we reversed the sign of the effect sizes extracted for nearest-neighbor studies to make them comparable to those extracted for all other studies representing the response to increasing wetland or forest amount (Gurevitch and Hedges 1993).

Second, the relationship between sampling effort used to measure population abundance of a given species and the size of wetlands may influence the wetland ES observed. Studies in which sampling effort increased in proportion to wetland size will observe a positive relationship between wetland size and abundance, simply because more area is searched in larger wetlands. If wetland patch size is positively correlated with total wetland amount in a landscape, this will inflate the apparent effect of wetland amount because more wetland was sampled in landscapes containing more wetland. Therefore, we categorized studies by the species sampling approach as, (1) area-independent, where sampling effort was consistent across sampled wetlands, (2) area-dependent, where sampling effort increased in proportion to the wetland area, or (3) unknown, where the sampling effort was unknown and could not be obtained by contacting authors. When a study used a combination of more than one of these methods, we selected the sampling method that accounted for the majority of the species observations.

Third, the effect of wetland amount in a landscape (wetland ES) could vary depending on whether the sampled wetland was included in the calculation of wetland area in a landscape (wetland amount). Prugh (2009) found that measures of habitat amount in a

landscape, including area-based buffers, nearest-neighbor distances, and connectivity, were better predictors of occupancy when the focal patch area was included in the model. Therefore, we expected a priori that studies that did not include the sampled wetland patch area in wetland amount would have a lower effect size compared to studies that did include the sampled wetland patch area.

Fourth, the wetland ES might vary depending on the population response measured for each species in a study. We included studies that measured relative abundance, relative density, or occupancy, and use the umbrella term “population abundance,” because these response variables are generally highly correlated. However, in a recent meta-analysis on population responses to landscape, patch, and within-patch variables, Thornton et al. (2011) found that, in some cases, effect sizes were larger for studies that measured abundance or density rather than occupancy. To determine whether the population response affected our results, we recorded the response type measured in each study and included it as a moderator variable.

Lastly, the effect of wetland amount (wetland ES) and/or forest amount (forest ES) may be confounded by the correlation between the two landscape variables. For example, if the amount of wetland and forest were positively correlated in a study, a positive forest ES estimate might be statistical artefact. Therefore, we recorded the correlation between wetland amount and forest amount in each study. If wetland amount and forest amount were measured at multiple spatial scales in a study, we calculated the correlation at their respective scales of effect. For example, if the scale of effect was 500 m for wetland ES and 1000 m for forest ES, we calculated the correlation between wetland amount measured at 500 m and forest amount measured at 1000 m.

Effect size calculations

We selected the Pearson correlation coefficient r between the population response and wetland or forest amount as our estimate of wetland ES and forest ES from each study. When a study reported Spearman's rank correlation coefficient (ρ), we converted ρ to r following Lajeunesse (2013). If studies did not report a correlation coefficient, we transformed published test statistics as follows. For studies with continuous measures of population abundance, we extracted r values by taking the square root of reported R^2 values from univariate linear regressions, and adding the sign of the slope. Note that we did not use partial R^2 values or slope coefficients from multiple regression, AIC values, or results from multivariate statistics (Hullett and Levine 2003, Lajeunesse 2013); in these cases, we used raw data provided by authors to calculate r . When raw data were available for continuous measures (abundance or density), we calculated r for those species with occurrence rates ≥ 0.7 . Continuous data sets with

occurrence rates ≤ 0.7 did not meet normality assumptions of r ; in this case, we converted raw abundance data to occupancy data to determine an effect size. For studies that measured species occupancy or reported means and variances between two groups (e.g., mean wetland amount in occupied vs. unoccupied landscapes), we first calculated the standardized mean difference (ES_{sm}) following Gurevitch and Hedges (1993). We then converted each ES_{sm} to r following Borenstein et al. (2009). We transformed all correlation coefficients to Fisher's z scale (ES_{Zr}) following Borenstein et al. (2009). Note that we were unable to incorporate detection probability estimates from occupancy studies into our effect size calculations because such methods are not yet developed for meta-analysis (Lajeunesse 2013).

The next step was to obtain accurate and comparable sample sizes across studies. Meta-analysis weights each study by its inverse variance, based on the assumption that studies with greater precision will provide a more accurate estimate of the true effect. The variance of ES_{Zr} is approximated as $V_{Zr} = 1/(n - 3)$, where n is the total sample size of the study (Borenstein et al. 2009). This gives more weight to studies with larger sample sizes; however, this may overweight studies with pseudoreplication, a common problem in landscape ecology (Eigenbrod et al. 2011). For example, within a given study area, studies that selected spatially independent wetlands in nonoverlapping landscapes at a landscape size (i.e., scale) based on a species' biology may have a lower apparent sample size than studies that sampled as many wetlands as possible without consideration of spatial independence. In the latter, the sample size would be inflated due to nonindependence of sample points. Therefore, we assessed the sample size of each study for pseudoreplication using process similar to that in Rytwinski and Fahrig (2012) as follows. Our assessment was based on the assumption that each data point should represent a spatially independent sample. We assumed that an independent sample was equivalent to an independent individual in a spatially independent sampling location, such that it was unlikely the same individual was sampled at more than one wetland. We considered studies to have independent samples, and therefore accurate sample sizes, in two situations. First, studies that selected nonoverlapping landscapes a priori based on the movement range of the species were assumed to be independent samples because it is unlikely that the same individual would be sampled in neighboring sites. Second, in studies where each landscape represented the area around a sampled individual (e.g., a nest), the number of landscapes was already equivalent to the number of independent individuals. For all other studies, we adjusted sample size. When the distance between two sampling locations (e.g., wetlands) was less than the linear home range or territory size of the species, the two locations were counted as a single sample. We obtained information on home range or territory size for each species from the primary

literature, theses and published species guides, which we collected in our previous meta-analysis (Quesnelle et al. 2014); any species lacking movement information was excluded from the current study. For studies that compared population abundance in sampling locations to randomly selected locations where the species was known to be absent, and spatial information on these random locations was not available, the sample size was the number of spatially independent sampling locations plus one (to account for all random locations).

After determining the adjusted sample size (n_{adj}) of each study, we calculated the inverse variance weight for each ES_{Z_r} as $w = n_{\text{adj}} - 3$ (Lipsey and Wilson 2001). Studies with $w < 1$ were excluded from the meta-analysis. We also classified effect sizes by taxonomic group at the class level (mammal, bird, reptile, and amphibian), and by order within each taxonomic group. Refer to Appendix A for studies included in the meta-analysis and associated country, species with taxonomy classification, effect sizes, adjusted sample sizes, and study design categories.

Meta-analyses

To assess the relative effects on wetland animal abundance of wetland amount and forest amount in a landscape, we used the estimates for each of wetland ES_{Z_r} and forest ES_{Z_r} calculated at their scale of effect (i.e., the largest ES_{Z_r} calculated from the range of scales measured in a study, as described previously). We conducted random-effects meta-analyses using the DerSimonian-Laird method (Borenstein et al. 2009) to determine the summary weighted-mean effect size of the overall population response of wetland species to wetland amount at the landscape scale and the summary weighted-mean effect size of the overall population response of wetland species to forest amount at the landscape scale. Under the random-effects model, the weight assigned (w^*) to each effect size is the inverse of the sum of two variance components $w^* = 1/(w + T^2)$, where w is the unique sampling variance for each study (within-study error) and T^2 is the pooled variance of the true effects across all randomly selected studies (between-studies variance; Borenstein et al. 2009). We also calculated the heterogeneity in true effects (Q statistic), which we compared against a chi-square distribution, to test whether the total variation in observed effect sizes (Q_T) was significantly greater than that expected from sampling error (Q_E).

We then tested whether moderator variables (study type, sampling effort, wetland patch area, response type, and taxonomic class) could explain variation in the effect sizes Q_M , i.e., $Q_T = Q_M + Q_E$, by performing univariate mixed-effects meta-analysis using restricted maximum-likelihood (REML) estimation of heterogeneity. If a moderator variable explained significant heterogeneity in the effect sizes, we would then subset our data by that moderator variable to control for its influence on the relative effects of wetland amount and

forest amount. To determine the relative effects of wetland and forest, we used a paired-sample t test to compare the mean z -transformed correlation coefficients between wetland animal abundance and each of these two landscape variables (i.e., mean wetland ES_{Z_r} – mean forest ES_{Z_r}). We used a paired-sample t test because wetland ES_{Z_r} and forest ES_{Z_r} were estimated for the same species within each study. We then performed a mixed-effects meta-regression to test whether the difference in effect size for wetland and forest for each study was confounded by the correlation between wetland amount and forest amount in the study.

To ensure that the results were not biased by the spatial scale selected in each study, we assessed whether the relative effects of wetland amount and forest amount were scale dependent (i.e., changed with scale). We used each pair of wetland ES_{Z_r} and forest ES_{Z_r} estimated at every spatial scale measured for each species in a study (Fig. 2, step 6). At each spatial scale, we calculated the absolute difference in effect size for wetland amount and forest amount (i.e., $|\text{forest } ES_{Z_r} - \text{wetland } ES_{Z_r}|$) to get the relative effect size. We then conducted linear mixed-effects regression with nested random effects using REML estimation. The response variable was the relative effect size and the predictor variable was $\log(\text{landscape scale})$ where the measured scale was in meters. The random variables were “study” to control for variation among study areas, and “species” nested within “study” to account for studies that measured multiple species responses at multiple scales. We tested if the relative effect size changed significantly with scale by using 95% highest posterior density (HPD95) intervals and P values generated from Markov chain Monte Carlo simulations ($n = 1000$ randomizations).

Lastly, we assessed publication bias by a rank correlation (Kendall’s tau) test of the relationship between ES_{Z_r} and n , along with visual inspection of a scatterplot between these two variables following Jennions et al. (2013). All analyses were conducted in R 3.0.1 (R Development Core Team 2013), using the packages metafor, lme4, and languageR.

RESULTS

Sixty-three of ~200 studies that examined the effect of wetland amount in a landscape on population abundance of wetland-dependent vertebrates met the inclusion criteria in this meta-analysis (Fig. 2). These 63 studies, from 12 countries, generated 330 effect sizes across 155 species (including seven species complexes). Studies were predominately from North America (46) and Europe (11), with remaining studies from Australia (3), South America (2), and Asia (1) (Appendix A). We obtained raw data from authors for 50 of the 63 studies to independently calculate an effect size when the relationship between population abundance and one of the landscape variables (wetland or forest amount) was not reported (9 studies), or when we could not extract an effect size directly from the analysis used in those studies

(multiple regression or partial R^2 (30 studies), AIC (three studies), species richness (three studies), multivariate analysis (one study), or other analysis types (e.g., GAM, generalized additive model; four studies). Occupancy data were used to calculate 255 of the 330 effect sizes, followed by abundance and density data for 72 and 3 effect sizes, respectively (Appendix A). The majority of studies (53) measured the amount of forest surrounding wetlands at the same spatial scale(s) as the amount of wetland in a landscape. For the remaining 10 studies, we measured the amount of forest surrounding wetlands using geographical coordinates (Fig. 2, step 5).

The summary weighted-mean effect size for wetland amount from a random-effects meta-analysis across all taxa was 0.10 (95% CI: 0.079, 0.129; $n = 330$), indicating an overall weak, positive effect of wetland amount in a landscape on wetland animal population abundance. The overall heterogeneity was $Q = 659.19$ ($P < 0.0001$), indicating highly significant variation in species responses to wetland amount. The summary weighted-mean effect size for forest amount from a random-effects meta-analysis across all taxa was 0.08 (95% CI: 0.048, 0.114; $n = 330$), indicating an overall weak, positive effect of forest amount in a landscape on wetland animal population abundance, of the same magnitude as the overall effect of wetland amount. The overall heterogeneity was $Q = 1158.13$ ($P < 0.0001$), indicating highly significant variation in species responses to forest amount. The correlation between wetland amount and forest amount across landscapes within a study was generally low, but varied widely across studies (mean $r = -0.02$, range $r = -0.84$ – 0.80 ; Appendix B: Fig. B1). There was no strong evidence of publication bias, as there was a weak relationship between wetland ES_{Zr} and sample size (Kendall's tau = -0.001 , $P = 0.99$), and between forest ES_{Zr} and sample size (Kendall's tau = 0.023 , $P = 0.54$). Moreover, scatterplots between wetland ES_{Zr} and sample size, as well as forest ES_{Zr} and sample size, showed that effect sizes were symmetrically distributed around the summary effect and produced a funnel shape with greater variation in studies at low sample sizes, as expected (Appendix C: Figs. C1 and C2).

Mixed-effects meta-analysis across all taxa ($n = 330$) showed that none of the study design moderators (study type, sampling effort, sampled wetland area, or response type) explained significant heterogeneity in the effects (for study type, $Q_M = 0.66$, $P = 0.418$; for sampling effort, $Q_M = 5.85$, $P = 0.055$; for sampled wetland area, $Q_M = 2.83$, $P = 0.092$; for response type, $Q_M = 0.74$, $P = 0.69$; Appendix D). Therefore, we did not control for study design. The effect of wetland amount in a landscape on wetland animal abundance varied by taxonomic class ($Q_M = 30.57$, $P < 0.0001$; Appendix D). The weighted-mean effect size of wetland amount for mammals and birds was greater than that of amphibians and reptiles (Fig. 3). Similarly, the effect of forest amount in a landscape on animal abundance

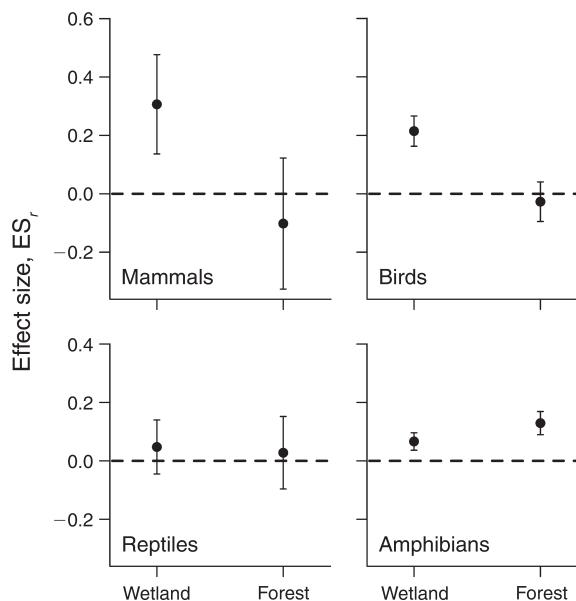


FIG. 3. Population-level responses of wetland animal classes to wetland amount and forest amount in a landscape. Points represent mean-weighted effect sizes (z -transformed Pearson correlation coefficients, r) from mixed-effects meta-regressions; error bars indicate 95% confidence intervals.

varied by taxonomic class ($Q_M = 18.71$, $P = 0.0003$; Appendix D). However, the effect of taxa on the forest amount effect was opposite to the effect of taxa on the wetland amount effect; the weighted-mean effect size of forest amount for mammals and birds was lower than that of amphibians and reptiles (Fig. 3). Therefore, we tested whether the mean effect sizes of wetland amount and forest amount were significantly different for each taxonomic class separately.

For mammals, the effects of wetland amount and forest amount were not significantly different ($t = 1.975$, $df = 6$, $P = 0.096$); however, the lack of a significant difference is probably due to the low sample size ($n = 7$). For birds, the effect of wetland amount was more important than the effect of forest amount ($t = 7.578$, $df = 97$, $P < 0.0001$). The correlation between wetland amount and forest amount in a landscape across studies for birds was low (mean $r = -0.14$, range $r = -0.56$ – 0.80 ; Appendix B: Fig. B2). The effect size for wetland amount on birds was not related to the correlation between wetland amount and forest amount in a study ($Q_M = 0.06$, $P = 0.81$). Therefore, the larger effect of wetland amount than forest amount on birds was not a statistical artefact of the negative correlation between wetland amount and forest amount in a landscape.

For amphibians (anurans and caudates), the effect of forest amount was more important than the effect of wetland amount ($t = -4.129$, $df = 204$, $P < 0.0001$). The correlation between wetland amount and forest amount in a landscape across studies for amphibians was low (mean $r = 0.04$, range $r = -0.84$ – 0.69 ; Appendix B: Fig.

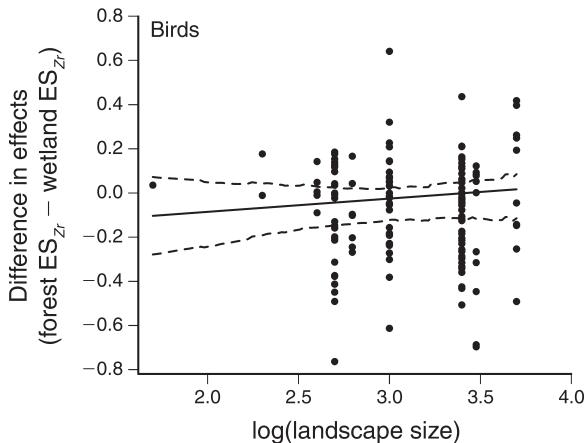


FIG. 4. Difference in effects of wetland and forest amount ($|\text{forest ES}_{Z_r} - \text{wetland ES}_{Z_r}|$) on wetland bird population abundance at increasing spatial scales (log-transformed landscape size, originally measured as radius in meters). The solid line is the fitted relationship from a mixed-effects model and dashed lines are 95% highest posterior density intervals obtained from Markov chain Monte Carlo simulations.

B3). The effect size of forest amount was not related to the correlation between wetland amount and forest amount in a study ($Q_M = 3.15$, $P = 0.08$). In other words, the larger, positive effect of forest amount, rather than wetland amount, on amphibians was not confounded by a correlation between forest amount and wetland amount. For reptiles (turtles and water snakes), the effects of wetland amount and forest amount were not significantly different ($t = -0.168$, $df = 19$, $P = 0.868$), although the sample size was low ($n = 20$).

Because the effects of wetland amount and forest amount varied by taxonomic class, we tested whether the relative effects were scale dependent within each taxon separately. For mammals, there were too few effect sizes ($n = 7$) to meaningfully test whether the relative effects changed with spatial scale. For birds, the relative effects of wetland amount and forest amount did not change with spatial scale from 50 to 5000 m (slope = 0.060; HPD95lower = -0.075, HPD95upper = 0.145; MCMC-derived $P = 0.544$). The fitted model for birds showed that wetland amount was more important than forest cover at all spatial scales (Fig. 4). For amphibians, the relative effects of wetland amount and forest amount did not change with spatial scale from 100 to 6000 m (slope = -0.006; HPD95lower = -0.025, HPD95upper = 0.009, MCMC-derived $P = 0.412$). The fitted model showed that forest amount was more important than wetland cover at all spatial scales (Fig. 5). For reptiles, there were too few effect sizes ($n = 20$) to meaningfully test whether the relative effects changed with spatial scale.

DISCUSSION

For wetland birds, our results support our a priori expectation that the amount of wetland in a landscape is

more important than landscape matrix quality (Fig. 3). The effect on bird population abundance of wetland amount was consistently strong and positive across spatial scales (Fig. 4). This is not surprising, because all breeding-season activities (foraging, mating, nesting) are carried out at or near the edge of wetland habitat. The positive effect of wetland amount is most likely due to higher food and nesting site availability in landscapes with more wetland (Tozer et al. 2010). The effect on bird population abundance of forest amount was relatively weak and confidence intervals overlapped zero (Fig. 3). This suggests that the quality of the surrounding matrix is less important than the total area of wetland in a landscape for wetland birds, and is consistent with previous studies measuring the effects of forest, agriculture, and development in a landscape relative to the effect of wetland amount (Gibbs and Kinkel 1997, Shriver et al. 2004, Valente et al. 2011, Quesnelle et al. 2013). This explanation is plausible because birds do not interact directly with the surrounding matrix during movements between wetlands; therefore, dispersal mortality is likely to be low regardless of matrix quality. In support of this notion, a recent meta-analysis found a very weak effect of road and/or traffic density on bird population abundance (Rytwinski and Fahrig 2012).

However, we acknowledge that our measure of landscape matrix quality (forest amount) was not perfect, because matrix quality can depend on the composition of the non-forest part of the matrix. For example, urbanization generally has stronger negative effects on abundance of wetland-dependent species than does agriculture (Gagné and Fahrig 2007, Smith and Chow-Fraser 2010). Moreover, Ward et al. (2010) found negative effects of urban development on wetland bird

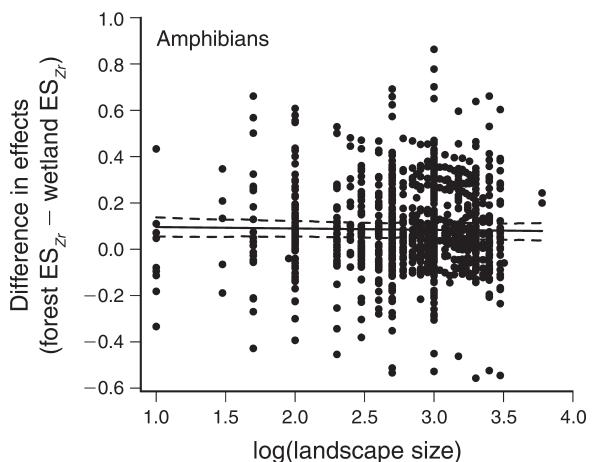


FIG. 5. Difference in effects of wetland and forest amount ($|\text{forest ES}_{Z_r} - \text{wetland ES}_{Z_r}|$) on amphibian population abundance at increasing spatial scales (log-transformed landscape size, originally measured as radius in meters). The solid line is the fitted relationship from a mixed-effects model and dashed lines are 95% highest posterior density intervals obtained from Markov chain Monte Carlo simulations.

abundance despite no wetland loss. These effects were attributed to changes in hydrology and vegetation structure of the wetland (Ward et al. 2010). Because such changes are one of the main mechanisms by which matrix quality influences local patch biodiversity (Driscoll et al. 2013), we may have underestimated the effect of matrix quality, e.g., urbanization, on wetland biodiversity. On the other hand, in a study designed to separate the independent effects of wetland amount and urbanization, wetland amount in the surrounding landscape was found to have greater positive effect on wetland vegetation communities and water quality than did the negative effect of urbanization (T. Patenaude, A. C. Smith, and L. Fahrig, *unpublished manuscript*). Therefore, including urbanization in the measure of landscape matrix quality might increase the effect of matrix quality on birds, but it is unlikely to render matrix quality more important than wetland amount.

For wetland amphibians, our results did not support our a priori expectation that the amount of wetland would be more important than matrix quality; instead, forest amount was the more important predictor (Fig. 3) at all spatial scales (Fig. 5). In a qualitative review, Marsh and Trenham (2001) compared the relative effects of wetland amount (measured as distance to nearest pond) to effects of terrestrial habitat amount, measured as distance to forest, or as amount of pasture, shrubland, and forest in a landscape. Consistent with our results, Marsh and Trenham (2001) posited that the amount of useable terrestrial habitat in a landscape (equivalent to high-quality landscape matrix in our terminology) was a better predictor of amphibian population dynamics and abundance than wetland amount. To the best of our knowledge, our quantitative review is first to test their hypothesis and support their prediction that processes occurring outside wetland habitat better explain the population distribution of amphibians than does wetland availability in a landscape.

Forest amount had a larger effect than wetland amount on amphibian population abundance, likely because forest is terrestrial post-breeding habitat for many wetland-breeding amphibians. For those species, forest provides complementary summer foraging, refugia (aestivation), and/or overwintering habitat required to complete their life cycle (i.e., juvenile and adult life stages). Given that at least one breeding wetland is available, a landscape with more forest provides more complementary habitat, thereby supporting greater amphibian abundances (i.e., landscape complementation; Dunning et al. 1992). If the availability of complementary habitat provided by forests is limited, such that juvenile and adult stages do not survive to the next breeding season, local population sizes at breeding wetlands will be low despite high wetland amount in the landscape. It is also possible that the density of emerging juveniles in upland forest is higher in the forest that is accessible from the wetland. This higher density might

decrease survival, growth, and reproductive development of individuals (Harper and Semlitsch 2007, Berven 2009), reducing the overall population growth rate even if there is ample wetland habitat available. This is contrary to the general assumption that wetland breeding habitat has a greater influence on population dynamics of amphibians than does terrestrial habitat (reviewed by Marsh and Trenham 2001).

On the other hand, terrestrial habitat use would not explain a larger effect of forest amount than wetland amount on abundance of wetland-breeding amphibian species that do not require forest to complete their life cycle. To test whether forest amount is important independent of habitat use, we first classified each amphibian species included in the meta-analysis as a “forest species” or “non-forest species” using habitat accounts in the literature and field guides. We classified any species described as using forest during any part of its juvenile or adult stage as a forest species, so that any bias in testing the relative effects of wetland and forest amount was in the direction of wetland amount. We then compared the relative effects of wetland amount and forest amount for just the subset of non-forest species. We found that the overall mean effect of forest amount (0.083) was still larger than the mean effect of wetland amount (0.054), but the difference was nonsignificant ($t = -0.612$, $df = 64$, $P = 0.543$). This suggests that the amount of forest in a landscape has a positive effect on amphibian abundance beyond providing terrestrial habitat.

A second possible reason for the greater effect on amphibian population abundance of forest amount than wetland amount is the importance of dispersal mortality in affecting population abundance. Experimental field studies have shown that many amphibians, including several non-forest species, orient toward and prefer to move through forest during emigration from the breeding pond, avoiding open areas such as fields, pastures, and clearcuts (Rothermel and Semlitsch 2002, Patrick et al. 2006, Todd et al. 2009, Pittman and Semlitsch 2013). Moreover, these studies show that individuals move significantly greater distances in forest compared to open areas, presumably due to higher mortality in open areas (Rothermel and Semlitsch 2002, Popescu and Hunter 2011). Amphibians experience significantly lower desiccation rates in forests than in fields (Rothermel and Semlitsch 2002) because canopy cover and leaf litter lower temperature and increase humidity near the ground (Popescu and Hunter 2011). For example, wetland-breeding salamanders have significantly lower survival rates in clearcuts than in unharvested controls (Todd et al. 2014). An increase in dispersal mortality with decreasing forest cover in the landscape could lead to lower local (e.g., pond) population sizes, despite a high amount of wetland habitat.

In fact, demographic models for a range of wetland-breeding amphibians predict that factors that increase

mortality during the post-breeding stage, such as loss of post-breeding terrestrial habitat or high dispersal mortality, affect amphibian population dynamics more than factors that increase pre-metamorphic mortality, such as wetland loss (Biek et al. 2002, Vonesh and de la Cruz 2002, Salice et al. 2011). Since it is likely that reductions in the amount of surrounding forest in a landscape decrease survival rates of juveniles and adults, a larger effect on amphibian abundance of forest amount than wetland amount is therefore not surprising.

An alternative explanation for the effect of forest amount on amphibians is that forest in the surrounding landscape influences local wetland health. Forest cover may buffer wetlands from sedimentation and pollution, moderate wetland temperature and reduce evaporation rates, provide organic and inorganic matter, and maintain wetland hydrology and drainage patterns in a landscape (Richardson and McCarthy 1994, Findlay and Houlihan 1997, Semlitsch and Bodie 2003). In fact, the amount of forest surrounding 73 wetlands in southeastern Ontario was found to have a strong, positive relationship with multiple water and sediment quality parameters (e.g., nitrogen, phosphorus), even when controlling for local wetland size and other landscape variables, including wetland amount and road density in a landscape (Houlihan and Findlay 2004). If wetlands surrounded by more forest in a landscape are healthier, then local amphibian abundance would presumably increase.

On the other hand, a strong positive effect of forest cover in a landscape could result from a potentially confounding variable, if the variable were correlated with forest amount. Lack of independence among land cover categories is a well-established problem in landscape studies (reviewed in Allan 2004, King et al. 2005). For example, in forested ecoregions, the amount of forest cover in a landscape is generally negatively correlated with other landscape variables, such as crop cover, urbanization, and road density (Findlay and Houlihan 1997). Therefore, increasing forest cover may represent decreasing amounts of agricultural fertilizer and pesticide inputs in a landscape, which were found to be negatively correlated with amphibian abundance in 75 wetlands in southeastern Ontario (Houlihan and Findlay 2003). Similarly, because road and/or traffic density have strong negative effects on amphibian population abundance (Rytwinski and Fahrig 2012), it is possible that the positive effect of forest amount is simply a reflection of the forest vs. road correlation (i.e., amphibians respond positively to landscapes with low road density). However, in previous studies on wetland biodiversity, when forest amount and road density were included in models together (i.e., statistically controlled), both variables had near-significant effects (Findlay and Houlihan 1997, Houlihan and Findlay 2003), suggesting that forest and roads each have independent effects. This was confirmed in a study by

Eigenbrod et al. (2008), who selected sample landscapes such that forest amount and traffic density were not correlated. They found that the independent effect of forest cover on wetland-breeding anuran populations was about as large as the effect of traffic, but that the relative effects of these two variables varied with species. Therefore, we are confident that the strong, positive effect of forest amount that we detected in our meta-analysis is not a statistical artefact of a negative effect of roads. Lastly, it is possible that forest quality could be correlated with forest cover, if landscapes with low forest cover are also of lower quality (e.g., plantations, clearcuts). If this were true, then the positive effect of forest amount could reflect a positive effect of forest quality rather than forest amount. However, we have no reason to expect such a correlation or that it would be consistent across studies included in the meta-analysis. Overall, we cannot exclude the possibility that the strong positive effect on amphibians of forest amount occurred through a correlation with another landscape variable (e.g., cropland, roads), but we suggest that our results are likely not due to a correlation between forest amount and forest quality.

For wetland-dependent reptiles, our results suggest that populations of freshwater turtles and water snakes are limited by neither the distribution of wetlands nor the amount of high-quality matrix in a landscape (Fig. 3), indicating that some other factor limits their distributions. We suggest that access to complementary resources (landscape complementation) is limiting reptile populations. Like wetland-breeding amphibians, wetland reptiles require different habitats to complete their life cycle, which necessitates seasonal overland movements outside of wetlands. All freshwater turtles require terrestrial nesting habitat (Steen et al. 2012) and water snakes (and some turtles) typically overwinter in terrestrial habitats (Roe et al. 2003). However, these complementary habitats are usually fine-scale features not captured in coarse-scale resolution (>30-m) land cover data such as forest cover. For example, Marchand and Litvaitis (2004) found a positive relationship between the area of suitable nesting habitat within 30 m of wetlands and painted turtle abundance for wetlands along a gradient of forest amount.

It is also possible that road mortality may limit local reptile populations in landscapes with high road and/or traffic density, despite high wetland amount, high-quality matrix (i.e., forest), or availability of nesting sites or other complementary habitats. As road density increases in a landscape, it is unlikely that all complementary habitat occurs within a roadless area. In some landscapes, this could force all individuals of a local population to cross roads, resulting in very high mortality rates (e.g., Aresco 2005). Reptiles have delayed sexual maturity and low reproductive rates, which means that their populations recover slowly from adult mortality events. In fact, nesting migrations increase female turtle vulnerability to road mortality,

which is considered to be the most significant threat to freshwater turtle population persistence (Steen et al. 2012). Similarly, road mortality is suggested to significantly contribute to water snake declines (Roe et al. 2006), with females possibly more susceptible due to greater movements in search of parturition sites (Attum et al. 2007). In line with our results, a recent meta-analysis found that amphibians and reptiles were more susceptible to the negative effects of roads than were mammals and birds (Rytwinski and Fahrig 2012).

Our review suggests that the amount of wetland habitat in a landscape is not limiting to wetland-dependent amphibians or reptiles. This is surprising because metapopulation structure, based on the assumption that wetland patches contain local populations, is widely assumed to apply to the population dynamics of these animals (e.g., Cosentino et al. 2010, Werner et al. 2009, Heard et al. 2012). In contrast, a meta-analysis by Prugh et al. (2008) found that amphibians and reptiles in general have relatively weak responses to patch area effects compared to birds and mammals. As discussed previously, unlike wetland-dependent birds and mammals, many amphibians and reptiles require different habitat types to complete their life cycles, which necessitates regular overland movements, increasing the importance of matrix quality (e.g., forest cover, roads). In fact, if the availability of complementary habitat near a given wetland is low, amphibians must move larger distances to find them (Laan and Verboom 1990, Reh and Seitz 1990), and similarly turtles will need to move longer distances to reach nesting habitat (Baldwin et al. 2004) or overwintering sites (Harden et al. 2009). These longer movements increase the probability of dispersal mortality due to factors such as desiccation, predation, or road mortality. Our results imply that the population distribution of wetland-dependent amphibians and reptiles is more strongly related to landscape matrix quality than to the availability of wetland in a landscape. Specifically, the quantity of and/or access to complementary terrestrial habitat is limiting.

Lastly, the concept of “the matrix” and matrix quality is highly variable and is used in different ways in ecology. From a traditional island biogeography and metapopulation perspective, the matrix is viewed as inhospitable and homogeneous non-habitat. In contrast, in landscape ecology the matrix is viewed as a heterogeneous mosaic of land cover types that vary in their degree of influence on dispersal, resource availability, and abiotic edge effects (i.e., low to high matrix quality; reviewed in Driscoll et al. 2013). There is no standardized way of measuring the quality of the matrix. Here we used forest cover as an index of matrix quality for wetland biodiversity (Findlay and Houlihan 1997). We did not use a more complicated measure of matrix quality because forest is the only land cover type that is reliably available worldwide from remote sensing data (Sexton et al. 2013). Moreover, forest cover was the land

cover type most commonly measured in included studies. If reliable land cover data were available for all of our study locations, we could have indexed decreasing matrix quality using a combined measure of road density, crop cover, and/or urbanization. Instead, we assumed a negative correlation between forest cover and these matrix variables, so that forest cover could be used as an index of increasing matrix quality.

Although the species that we included in our meta-analysis are all “wetland-dependent,” our results show that this characterization can be misleading for conservation management, particularly for amphibians and reptiles. Our results suggest that management strategies that focus mainly on wetland habitat are likely to often overestimate the capacity of a landscape to support populations of wetland-dependent amphibians and reptiles, at least in forested ecoregions. In fact, we suggest that we should stop thinking of these species as wetland species because that designation is harmful to their persistence.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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