Imperfect detection biases extinction-debt assessments

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Abstract
Freshwater ecosystems have been substantially altered, threatening the survival and recovery of aquatic species at risk. Estimating the likelihood and magnitude of future extinctions (extinction debt; ED) is integral for conserving biodiversity and requires accurate species composition lists. Using species-area relationships, we estimated ED for fishes in historically disturbed wetlands in the Lake Erie basin. Then, we used simulated data sets to assess how ED varied when species lists used to derive species-area relationships had an increasing proportion of undetected species. When species lists were incomplete, ranging from 0.99 to 0.75, 15% fewer wetlands were estimated to have species in ED and, on average, 50% fewer species were expected to go extinct per wetland. Imperfect detection ultimately biased conservation prioritization among wetlands. Our findings suggest that if imperfect detection is not accounted for when projecting future extinctions, the severity of future species loss across a landscape, and the subsequent need for immediate restorative action, can be greatly underestimated.

Keywords
extinction risk, freshwater fish, sampling bias, undetected species

1 | INTRODUCTION

A third of aquatic species are threatened with extinction globally (Collen et al., 2014), largely attributed to habitat degradation, loss, and fragmentation (Jackson, Loewen, Vinebrooke, & Chimimba, 2016; Schindler & Smol, 2006). To prevent further declines in freshwater biodiversity, risk assessments are required to identify vulnerable species and prioritize restoration efforts. Extinction-debt (ED) analysis can be used to predict whether past habitat loss will result in future species losses (e.g., Báldi & Vörös, 2006; Bonnmarco, Lindborg, Marini, & Öckinger, 2014), thus playing an important role in quantifying extinction risk and guiding conservation actions. Such lagged extinctions are quantified by comparing species–area (S–A) relationships or metapopulation dynamics across space and time (e.g., Cowlishaw, 1999; Helm, Hanski, & Pärtel, 2006; Lira, Ewers, Banks-Leite, Pardini, & Metzger, 2012; Newmark, Jenkins, Pimm, McNeally, & Halley, 2017). For example, several studies have used S–A curves to infer time-delayed extinctions after significant habitat loss in grassland systems (e.g., Brooks et al. 1999; Cousins 2009; Bagaria et al. 2018). Conversely, S–A curves and population dynamics (e.g., incidence function models) can be used to estimate immigration credits, which assume that a given area has the capacity to support a net gain in species over time (Hanski & Ovaskainen, 2000; Cristofoli & Mahy, 2010; Jackson & Sax 2009; Kolk, Naaf, & Wulf, 2017; Lira, de Souza, & Metzger, 2019).

Extinction debt has become increasingly used to inform conservation policy (e.g., Cowlishaw, 1999;
Hanski & Ovaskainen, 2002) and species/resource management (Wearn et al. 2012; Newmark et al., 2017). For example, ED estimates were used to prioritize restoration efforts across a landscape for African primates (Cowlishaw, 1999) and tropical birds (Newmark et al., 2017). Additionally, Semlitsch, Walls, Barichivich, and O’Donnell (2017) suggested multiple management approaches to recover declining amphibian populations, each of which address a hypothetical process underlying lagged extinctions (i.e., individual, population, or metapopulation). ED analysis has also been used to provide evidence to inform environmental licensing assessments for hydropower dams (Jones et al. 2016).

Interpretations of single-species and community dynamics to estimate ED can, however, be biased by sampling and analytical methods that do not account for imperfect species detection (Guillera-Arroita, 2017). While imperfect detection can be addressed with robust sampling methods (e.g., multi-gear sampling), occupancy-based models, and rarefaction-based richness estimates (e.g., Chao & Chiu, 2016; Gotelli & Chao, 2013), ED studies based on S–A relationships generally use observed species counts and/or museum records without consideration of undetected species (Bonebrake & Cooper, 2014; Newmark, 1996; Niissalo, Leong-Škorničková, Khew, & Webb, 2017). When based on current and historical data sets, differences in sampling effort and gear between time periods will further affect the comparability of species lists and bias S–A relationships and ED predictions. Lastly, habitat loss and fragmentation can skew species-abundance distributions by increasing the frequency of rare species (Hanski & Ovaskainen, 2002; Lira et al., 2012), which are often more difficult to detect (Royle & Nichols, 2003).

The influence of imperfect detection on ED estimates is rarely accounted for in the literature. Some ED studies use standardized sampling designs (Soga & Koike, 2013) or repeated surveys (Saar, Takkus, Pärtel, & Helm, 2012) to overcome imperfect detection, but do not provide evidence that species lists compiled with these approaches are complete. Also of concern, several ED studies opt to remove rare species from their species records to avoid inaccurate conclusions from poor catchability data (e.g., Duplisea, Frisk, & Trenkel, 2016; Lira et al., 2012). Disregarding imperfect detection can be problematic, as locally rare species have a lower probability of detection (Bayley & Peterson, 2001) but may also be at greater risk of extinction, due to demographic and stochastic factors (Hylander & Ehrlén, 2013). Even if weakly competitive rare species are at a lower risk of ED, excluding them in the analysis creates an incomplete picture of expected changes in species richness patterns over time.

While the role of imperfect detection on ED estimates has not been evaluated directly, several studies provide evidence that this area of research needs further attention, especially related to the use of species-area curves. Depending on the type of data set in question, there are six forms of the S–A curve commonly used in macroecology literature (Dengler, 2009), which differ predominantly on whether the S–A curve describes S–A relationships or species-sampling relationships. Due to their mode of construction, the influence of imperfect detection may differ with each form of the S–A curve. Species-sampling relationships described by species-accumulation curves tend to overestimate ED estimates (Halley, Šgardeli, & Monokrousos, 2013; He & Hubbell, 2011), as they better reflect sampling inconsistencies than ecological processes. S–A or endemic-area relationships that assume passive-sampling may underestimate species loss (Chase, Blowes, Knight, Gertsner, & May, 2020). Additionally, imperfect detection can influence the slope and intercept for S–A curves (Cam et al., 2002); hence, not correcting for detection-error can bias conservation targets (Karenyi, Nel, Altwegg, & Sink, 2016). To ensure the validity of ED estimates as a conservation tool, we must better understand the role that incomplete species lists play on ED estimates measured with S–A relationships.

Recent work by Montgomery, Reid, and Mandrak (2020) estimated the risk of ED in freshwater fishes in the Lake Erie basin. We expand on this work to examine an important methodological consideration for extinction-debt studies using S–A relationships in general. To examine the role of imperfect detection on ED estimates, we used the same fish community data set to simulate incomplete species lists. We tested the hypothesis that imperfect detection changes the predicted frequency (number of wetlands) and magnitude (number of species) of ED. By showing that undetected species can influence ED estimates measured with S–A relationships, these results illustrate the importance of accounting for imperfect detection in quantifying future species loss, which can be of critical importance in prioritizing areas in need of conservation.

2 | METHODS

2.1 | Data set

Simulations were based on fish inventory data from 71 wetlands located across the north shore of Lake Erie, Ontario (Appendix S1). The data set included a total of 84 species (248,874 individuals) of which 50 are classified as wetland specialists (215,133 individuals). Data sources were Fisheries and Oceans Canada (DFO) and multi-gear...
sampling conducted in 2016 and 2017 (see Montgomery et al., 2020 for details).

In this study, we estimate ED by comparing present-day, relatively stable and unstable landscapes. Four approaches are commonly used to estimate ED (Kuussaari et al., 2009), three of which use the S–A relationship to compare species richness estimates in disturbed and reference conditions. Wetlands were classified as disturbed and unstable \( (n = 39) \) or undisturbed and stable \( (n = 32) \) based on their protected status (e.g., located within a national or provincial park), which was reflective of watershed stress (Montgomery et al., 2020). In our study system, protected and unprotected wetlands differ significantly by agricultural and development stress; unprotected wetlands occur in regions with a significantly higher percentage of agricultural land, urban land, population density, and road density within a watershed (Montgomery et al., 2020). Given the history of wetlands in southwestern Ontario that large, continuous areas of wetland have been lost and/or fragmented because of land-use change to agricultural and development land (Snell, 1987), we can assume that wetlands with higher surrounding agricultural land have experienced a greater loss in wetland area and continue to be disturbed by these stressors. Conversely, while protected wetlands may have historically reduced in size, we assume this to be relatively minimal and that legal protection provides a buffer against ongoing stressors. Thus, we expect that wetland fish communities in protected wetlands should have remained relatively stable and can be used to develop S–A curves to which we can compare S–A relationships in relatively unstable, unprotected wetlands.

2.2 Data simulations

Four approaches are commonly used to estimate ED (Kuussaari et al., 2009), three of which use the S–A relationship to compare species richness estimates in disturbed and reference conditions. In this study, fish community data in protected (stable) wetlands were used to develop an expected S–A relationship for species richness at a set coverage-based stopping rule (sample coverage). Specifically, \( S_{\text{rare}} = \sum_{i=1}^{k} f_i \) where \( f_i \) is the number of species represented by \( i \) individuals and \( i \) is the number of individuals starting at 1 and ending at a cut-off value \( k \), which denotes the frequency of rare species (frequency \( \leq k \)) and abundant species (frequency \( \geq k \)). We used a cut-off value of \( k = 10 \), a standard value used in empirical data sets (Gotelli & Chao, 2013).

\[
\hat{S}_{\text{ACE}} = S_{\text{abun}} + \frac{S_{\text{rare}}}{C_{\text{rare}}} + \frac{S_{\text{rare}} \gamma^2}{C_{\text{rare}}} \tag{1}
\]

where \( C_{\text{rare}} = 1 - \frac{1}{n_{\text{rare}}} \) is the coverage estimate, \( f_1 \) is the number of species represented by exactly one individual, \( S_{\text{rare}} = \sum_{i=k+1}^{k} f_i \) is the number of observed species in the rare species group, \( S_{\text{abun}} = \sum_{i=1}^{k} f_i \) is the total number of observed species in the abundant species group, and \( \gamma^2 \) is the square of the estimated coefficient of the variation of the species relative abundances (Gotelli & Chao, 2013). Species richness for each wetland and sample coverage was estimated using the package “iNEXT” in R (Hsieh, Ma, & Chao, 2019).
The Arrhenius (1921) power function was used to fit S–A curves:

$$S = kA^z$$

where S is the number of estimated species (estimated richness of wetland-specialist fishes using ACE), A is the wetland area (m²), z is the slope of the S–A curve, and k is the expected number of species per unit area. We calculated the nonlinear least-squares estimate of model parameters with the function “SSarhenius” in the R package vegan (Oksanen et al., 2018). For each S–A relationship, the goodness of fit was assessed using the coefficient of determination ($R^2$).

We assessed bias due to reduced sample completeness on: (a) species richness; (b) number of wetlands with species in ED; and, (c) magnitude of future species losses. For each sample coverage, we used Welch’s $t$ test (appropriate for unequal sample sizes and variances) to test for significant differences between wetland types in (a) estimated species richness and (b) undetected species richness. Undetected species richness was calculated as the difference between observed species richness and estimated species richness.

Ordinal ranking of wetlands based on ED analysis could be used to prioritize the allocation of resources among candidate restoration sites. We assessed the effect of imperfect detection on such an approach by comparing rankings of individual unprotected wetlands across sample coverages. Rankings were based on the magnitude of future species losses. We then calculated Spearman’s Rank correlation ($r_s$) to measure the direction and strength of association between the wetland rankings at each sample coverage when compared with the “full species list” of 0.99 sample coverage.

3 RESULTS

Across all sample coverages, unprotected wetlands had higher estimated species richness than protected wetlands (Figure 1). Species richness for both wetland types increased with sample coverage (Figure 1a). Declines in sample coverage from 0.99 to 0.75 reduced the mean difference between protected and unprotected wetlands species richness by 75%. Wetland fishes in protected wetlands had a positive S–A relationship and retained a significant slope and intercept across all six sample coverages (Table 1; Figure 2). The slope, intercept, and goodness of fit increased with an increase in sample coverage (Table 1; Figure 2). When species lists were derived from observed data, wetland area explained 57% of the variation in wetland specialist richness in protected wetlands.

Using observed data, a mean of 7.0 ($SD = 6.3$) wetland fishes are expected to go extinct over time in unprotected wetlands. As sample coverage decreased from 0.99 to 0.75, the mean magnitude of ED decreased more than half from 6.4 to 1.7 (Figure 3). Mean ED decreased by a third when sample coverage decreased from 0.99 to 0.95 (Figure 3). There was a strong, negative correlation between undetected species and ED ($r = -1.0, p = .003$).

As sample coverage decreased, a smaller proportion of wetlands was predicted to be in ED (Figure 4a). At 0.99 sample coverage, 92% of unprotected wetlands were predicted to be in ED and 8% in immigration credit. The proportion of sites predicted to be in ED decreased to 77% and immigration credit increased to 23% with a sample coverage of 0.75 (Figure 4a).
TA B LE 1 Parameter estimates (k and z) fit with the power function (Arrhenius, 1921) using the observed species richness and six species richness estimates standardized by sample coverage as a proportion (0.75, 0.80, 0.85, 0.90, 0.95, 0.99) of the community richness, from protected wetlands in Lake Erie basin.

| Sample coverage | k    | SE  | p-value | z    | SE  | p-value | $R^2$ |
|-----------------|------|-----|---------|------|-----|---------|-------|
| 0.75            | 1.52 | 0.51| .04     | 0.11 | 0.035| .004    | .162  |
| 0.80            | 1.18 | 0.54| .04     | 0.11 | 0.034| .003    | .178  |
| 0.85            | 1.22 | 0.52| .02     | 0.12 | 0.32 | .0006   | .246  |
| 0.90            | 1.38 | 0.52| .013    | 0.13 | 0.28 | .0001   | .329  |
| 0.95            | 1.57 | 0.54| .007    | 0.13 | 0.26 | 1.29E−05| .414  |
| 0.99            | 2.46 | 0.88| .009    | 0.13 | 0.27 | 4.28E−05| .397  |
| Observed richness| 2.16 | 0.86| .017    | 0.16 | 0.29 | 7.23E−06| .570  |

Abbreviation: SE, standard error.

FIGURE 2 Log10-log10 species-area relationship fit with the power function (Arrhenius, 1921) for wetland-specialist fishes in protected (open circles, dashed line) and unprotected (closed circle, dashed line) wetlands in the Lake Erie basin. Using an abundance-based coverage estimator (Chao & Jost, 2012), species richness was standardized by the degree of sample completeness (a proportion of the total number of individuals observed): (a) 0.75; (b) 0.80; (c) 0.85; (d) 0.90; (e) 0.95; (f) 0.99; (g) observed species. The slope and intercept increased with increasing sample coverage (panel a to f) for both protected and unprotected wetlands. As sample coverage increased, the difference between predicted species (derived from the S–A relationship for protected wetland) and estimated species (derived from the S–A relationship for unprotected wetlands) increased, leading to a higher magnitude of extinction debt.
The order of sites ranked by magnitude of ED differed with variation in the number of undetected species in a species list. For example, at 0.99 sample coverage, the top three wetlands with the most predicted extinctions were the 8th, 18th, and 30th highest, when using a sample coverage of 0.75 (Figure 4b). When compared with 0.99 sample coverage, all rankings were positively correlated and statistically significant (Table 2). As the difference between 0.99 and each sample coverage increased, an agreement between rankings for each wetland decreased. The difference in wetland ranking was small between 0.95 and 0.99 and moderate between 0.75 and 0.99.

4. DISCUSSION

Using simulated species data sets developed from a large-scale wetland-fish inventory, this study demonstrated that imperfect detection influences ED estimates. Specifically, ED analysis based on species list with undetected species underestimated the predicted frequency (number of wetlands) and magnitude (number of species) of ED across a landscape. This pattern underscores the importance of accounting for undetected species through sufficiently robust sampling or statistical adjustments to strengthen its use as a conservation tool.

4.1 Effect of incomplete species lists on S–A curves

This study revealed that incomplete species lists affect the slope, intercept, and goodness of fit for the S–A curve.
relationship of wetland-specialist fishes. As sample coverage increased, the intercept of the S–A curve for protected and unprotected wetlands increased. Similarly, Borges, Hortal, Gabriel, and Homem (2009) found that richness estimates with fewer undetected species resulted in significantly higher intercepts for S–A relationships. Increased sample coverage also led to steeper S–A curves, which demonstrates that undetected species negatively affect the rate of species increase with wetland area. Likewise, Cam et al. (2002) found that richness estimates that incorporate detection probability had steeper slopes compared with observed data. Further, model fit increased with sample coverage, suggesting that wetland area explained more variation in species-richness patterns when undetected species were accounted for. These findings support previous findings that imperfect detection can influence the slope and intercept for S–A curves; hence, not correcting for detection error can bias conservation targets that rely on S–A curves (Karenyi et al., 2016).

4.2 | Effect of incomplete species lists on extinction-debt estimates

We found that imperfect detection leads to decreased mean ED and fewer sites with fishes in ED. At 0.99 sample coverage, there was no significant difference in undetected species between protected and unprotected wetlands, yet species-richness estimates were significantly different ($p = 4.72^{-5}$). A lack of significant difference in undetected species suggests that differences in species-richness estimates and, ultimately, the magnitude of ED estimates, at this level of sample completeness are not biased by sampling inconsistencies (undetected species) between protected and unprotected sites and, instead, reflect underlying ecological patterns. These findings imply that imperfect detection can act as a confounding factor and mask the extent of future extinctions.

4.3 | Conservation implications

ED estimates support the prioritization of conservation resources across a landscape. Sites can be pragmatically ranked by the magnitude of ED, with the assumption that resources should be allocated to sites with the most species expected to go extinct. If heterogeneous detection probabilities across a landscape are not accounted for, imperfect detection will influence the magnitude of ED differently for each site, thereby changing the order in which sites are ranked and the number of sites where extinction is expected. Differences in rank position across sample coverages and the decrease in correlation association suggests that imperfect detection can influence conservation prioritization. To maximize conservation resources, it is important that remedial efforts be allocated toward sites in the greatest need for restoration and that the identification of these sites is not influenced by incomplete surveys.

4.4 | Study limitations

Our results suggest undetected species will lead to the underestimation of future species loss. The exact form of this relationship is likely more complicated than presented in our study, as we did not incorporate heterogeneous detection probabilities into simulations. Rather than assuming detection probabilities to be constant, detection probabilities should be expected to vary among populations, species, and sampling gear, and along environmental gradients (Lahoz-Monfort, Guillera-Arroita, & Wintle, 2014). Detection probability may also differ between groups (e.g., stable vs. unstable) because of differences in sampling methods. For example, high-quality, historical data often do not exist or are collected with dissimilar methods and effort as current surveys (Boakes et al., 2010; Hortal, Jimenez-Valverde, Gomez, Lobo, & Baselga, 2008) and may be missing important count data (Semlitsch et al., 2017). Further, detection probability may be influenced by environmental disturbances and species most impacted by these disturbances may be most difficult to detect. Therefore, imperfect detection likely has a larger impact on ED estimates when there are differences in sampling methods and environmental variables between sites that may be correlated with imperfect detection.

4.5 | Recommendations

The accuracy of ED estimates using S–A relationships could be improved through a combination of refined sampling and statistical analysis. Optimal sampling design should incorporate multiple gear types that may target different species (e.g., Haynes et al. 2013; Wedderburn, 2018), seasonality (e.g., Rook, Mandrak, Reid, & Barnucz, 2016), and repeat sampling (Samarasin, Reid, & Mandrak, 2017). While our simulations were built on the assumption that all species have random, equal spatial distributions, species abundance and spatial aggregation can, in fact, influence survival and detectability, shaping the S–A curves (Cencini, Pigolotti, & Munoz, 2011; Yamaura et al., 2016) and, consequently, the magnitude of ED. Where possible, standardized
sampling approaches should reflect expected patterns of species density and distribution in different habitats (Borges et al., 2009).

If sampling effort is insufficient to achieve nearly complete samples that reflect underlying species distribution patterns, then statistical adjustments should be made to ensure undetected species do not bias future species loss. At minimum, species lists can be extrapolated/interpolated to standardize sampling efforts across sites by sample coverage (e.g., Hsieh et al., 2019). If repeat survey data is available, model-based estimators that incorporate imperfect species detection can be used to improve species richness estimates (e.g., Dorazio & Royle, 2005).

### 4.6 Conclusion

We demonstrate that without consideration of undetected species, future species loss may be underestimated and prioritization of wetlands for future management and restoration will be affected by the level of sampling completeness. Appropriate adjustments before or after surveys should account for false negatives and reduce the bias of ED to allow ecological processes to be evaluated free of sampling artifacts. Through analytical-simulation, this study provides a first step toward illustrating the potential bias of undetected species on ED. Follow-up field experimentation, or pseudo data sets representing different rank-abundance curves, would help expand knowledge of this bias under multiple scenarios.

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### CONFLICT OF INTEREST

The authors acknowledge that there are no known conflicts of interest.

### AUTHOR CONTRIBUTIONS

Fielding A. Montgomery, Scott M. Reid, Nicholas E. Mandrak conceived and designed the analysis, Fielding A. Montgomery collected the data, Fielding A. Montgomery, Scott M. Reid contributed data or analysis tools, Fielding A. Montgomery, Scott M. Reid performed the analysis, Fielding A. Montgomery, Scott M. Reid, Nicholas E. Mandrak wrote the paper.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from DFO. Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the corresponding author with the permission of DFO.

### ETHICS STATEMENT

This manuscript describes original work, has not been published, and is not under consideration for publication elsewhere.

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SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section at the end of this article.

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