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**Comparative analysis of abundance-occupancy relationships
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2 Comparative analysis of abundance-occupancy relationships for species-at-
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Abstract

The abundance-occupancy relationship is one of the most well-examined relationships in ecology. At the species level, a positive association has been widely documented. However, until recently, research on the nature of this relationship at broad taxonomic and spatial scales has been limited. Here, we perform a comparative analysis of 12 taxonomic groups across a large spatial scale (Canada), using data on Canadian species at risk: amphibians, arthropods, birds, freshwater fishes, lichens, marine fishes, marine mammals, molluscs, mosses, reptiles, terrestrial mammals and vascular plants. We find a significantly positive relationship in all taxonomic groups with the exception of freshwater fishes (negative association) and lichens (no association). In general, our work underscores the strength and breadth of this apparently fundamental relationship and provides insight into novel applications for large-scale population dynamics. Further development of species-independent abundance-occupancy relationships, or those of a similar nature, might well prove instrumental in serving as starting points for developing species-independent reference points and recovery strategies.

Key words: population dynamics, species abundance, recovery targets, conservation strategies, mammals (*Mammalia*), amphibians (*Amphibia*)

Introduction

The relationship between the abundance of a species and its geographical range, more classically termed the abundance-occupancy relationship, is one of the best-studied in macroecology (Brown 1984; Blackburn et al. 1997; Gaston et al. 1997, 2000; Zuckenberg et al. 2009). This fundamental association provides critical insight into the functionality of an ecological system and the nature of large-scale population dynamics (Brown 1984; Gaston 1997; Zuckenberg et al. 2009).

Common within the voluminous abundance-occupancy literature is the existence of both positive interspecific and intraspecific abundance-occupancy relationships that appear to be robust regardless of taxon, habitat type or life-history strategy (Brown 1984; Gaston and Lawton 1990; Zuckenberg et al. 2009). Initial investigations focused primarily on associations between abundance and distribution within species (Gaston 1996). Owing to the consistency and strength of the relationship within and among closely related species, this approach has been invaluable in providing a foundational understanding of how abundance is related to area of occupancy (Gaston 1996; Blackburn et al. 1997).

As investigations into the abundance-occupancy relationship progressed, researchers recognized the value of shifting research towards both developing a better understanding of the boundaries of the relationship (at what scales does the relationship break down?) and of investigating its potential for understanding population dynamics at much broader scales than have typified work in the past (Gaston 1996). Some studies have undertaken this challenge at either a large spatial scale (Blackburn et al. 1997; Zuckenberg et al. 2009) or at broad generalized taxonomic groupings (Blackburn et al.

1997), but those that include both (large spatial scales and broad groupings) are those likely to be most instructive in uncovering the outer bounds of the relationship. Blackburn et al. (1997) reported a positive relationship among British mammals and birds when grouped at broad taxonomic classification, whereas Zuckenberg et al. (2009) documented a similar association among songbirds in the U.S. state of New York. Even broader meta-analytical approaches exist that delve into the finer details of the relationship, such as that by Blackburn et al. (2006) who examined different influences on the effect size of the relationship (e.g. sample size, geographic distribution, habitat type, scales of abundance/distribution). Although these studies have established an empirically promising basis for increasing the breadth of abundance-distribution analyses, they have only begun to reveal the full potential of adopting broad spatial and taxonomic approaches to the study of this relationship.

To further explore the dynamics, limits, and boundaries of the abundance-occupancy relationship, the present study comprises a comparative analysis of twelve broad taxonomic groups examined over an uncommonly large spatial scale (the country of Canada). Specifically, we test the hypotheses that (i) abundance is positively associated with area of occupancy among (not simply within) species and (ii) the form of the relationship between abundance and occupancy does not differ among taxonomically disparate groups (e.g., lichens, arthropods, vertebrates). An additional objective is to explore the potential utility of these analyses in developing conservation management.

Materials and Methods

Occupancy and Abundance Data

Abundance and occupancy data were collated for 477 species at risk in Canada. The data were obtained directly from species status assessment reports published by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), available on the Species at Risk Public Registry (<http://www.registrelep-sararegistry.gc.ca>). For each species that COSEWIC assessed as endangered, threatened or of special concern, we recorded the occupancy, abundance, and taxonomic affiliation. The taxonomic groupings are based on a pre-assigned COSEWIC classification scheme which groups the species into 12 broad taxonomic categories: amphibians, arthropods, birds, freshwater fishes, lichens, marine fishes, marine mammals, molluscs, mosses, reptiles, terrestrial mammals, and vascular plants.

In accordance with similar literature, the occupancy estimates in COSEWIC's reports (which were those used here) were the estimated areas of occurrence, as reflected by an index of area of occupancy (IAO) (Gaston and Fuller 2009). Both abundance and occupancy estimates conform with criteria established by the International Union for the Conservation of Nature (IUCN), for which area of occupancy is the actual area that a species or population occupies within its extent of occurrence and abundance is the estimated number of mature individuals for a single species or population (IUCN Standards and Petitions Subcommittee 2014). COSEWIC's estimate of area of occupancy is a measure of the number grid cells occupied, using a cell size of 2km² and, in some specific circumstances, a size of 1km² (COSEWIC 2013). If estimates of either occupancy or abundance were unavailable, the species was excluded from the analysis.

When an estimate was provided as a range in the species status report, the mid-range value was used here.

Analysis

We compared six different models of varying taxonomic scale and model complexity (see Table 1). The simplest was a basic linear regression with occupancy as a function of abundance for the entire data set. We then examined whether the abundance-occupancy relationship differed between taxonomic groups by applying a mixed-effects model with taxonomic group as a random effect. In this model, occupancy is still a function of our fixed effect (abundance) but the random effect (taxonomic group) allows for the detection of taxon-specific relationships. The mixed-effects models were run twice: (1) random intercept and (2) both a random intercept and random slope. The first of the two mixed-effects models maintains a fixed slope but allows for variation in the intercept for each taxonomic group. The second mixed-effects model incorporates an additional level of variation as it allows for variation in both the intercept and slope for each taxonomic group. To account for potential non-linearity that has been documented in some abundance-occupancy relationships, all models were also run with and without a squared abundance term (Gaston et al. 2006; Hui and McGeoch 2007).

For each model, non-significant variables were removed through stepwise model reduction, using ANOVA, following Zuur et al. (2009). The individual random effects were tested using 95% confidence intervals around the model means, after which slope and intercept estimates were extracted for the significant relationships. To normalize our data, we tested two common transformations: logit and $\log_{10}$. Although recent literature suggests that a logit transformation for range size provides the best fit to normality

(Williamson and Gaston 1999, 2005), we found that optimal normality was achieved when we applied the $\log_{10}$ transformation. Thus, in the end both variables were $\log_{10}$ transformed for all of the analyses. All analyses were conducted with R v. 3.1.0 (R Core Team 2014).

Results

All six abundance-occupancy models were significant (Table 1). At the broadest ungrouped level (A and 2A), the regression model without the square abundance term (A) provided the best fit (ANOVA, $p < 0.001$), but explained relatively little variation ($r^2 = 0.07$) (Fig. 1).

The model that included a random intercept, random slope and squared abundance term resulted in the best fit of all six models (pairwise ANOVA comparisons with 2C: A: $p < 0.001$; B: $p < 0.001$; C: $p < 0.001$; 2A: $p < 0.001$; 2B: $p < 0.002$). A significant relationship between occupancy and abundance was evident for eleven of the twelve of the taxonomic groups; only one of the 95% confidence intervals included zero (lichens). Ten of these relationships exhibited positive associations whereas one was negative (freshwater fishes) (Fig. 2).

Discussion

The primary finding of the present study is that area of occupancy is related to abundance within and among phylogenetically diverse groups of species across extensive spatial scales. With the exception of freshwater fishes and lichens, and in accordance with other work undertaken at broad taxonomic and spatial scales (Blackburn et al. 1997; Zuckerman et al. 2009), all of the taxonomic groups exhibited significant positive abundance-occupancy relationships. The final model also included a negative square

abundance term that was less than one, suggesting that the relationship might not always be linear. These findings further underscore the robustness of the abundance-occupancy relationship, providing support to the hypothesis that a common ecological mechanism (related to factors such as habitat selection, niche breadth, rescue effect) might be responsible for driving the relationship across species (Blackburn et al. 2006; Borregaard and Rahbek 2010).

Contrary to expectations, neither freshwater fish nor lichens exhibited a positive relationship between occupancy and abundance. We suggest three possible reasons for this pattern: (1) the relationship is in fact not positive for these groups; (2) the relationship is positive though undetectable at the examined taxonomic level examined; or (3) the relationship is positive but measurement error has obscured the true relationship.

Even though the pattern of association for these two taxonomic groups appears to not be positive, based on our study, such a lack of association should be treated cautiously. Although instances of negative abundance-occupancy relationships have been reported at the species level (Gaston and Curnutt 1998; Webb et al. 2007), they are rare. Regarding the second hypothesis, it is possible that for these two taxonomic groups the present level of analysis was too broad to detect a meaningful relationship. That said, positive relationships were documented in all other taxonomic groups. Also, among the vertebrate groups, many have life-history strategies similar to those of freshwater fishes. Thus, we would not expect the taxonomic scale examined to be an issue for this group, however we cannot discount the possibility that taxonomic scale and (or) life history might be responsible for the absence of a relationship for lichens. The third hypothesis

(measurement error has obscured the true relationship) might be also represent a reasonable explanation. When collating estimates from COSEWIC species assessment reports, we found that estimates of occupancy for freshwater fish that had been assessed more than once often remained the same, an indication that the area of occupancy was likely estimated at the spatially static area of a lake or river system in which a fish species is present, as opposed to the actual dynamic area of occurrence.

Regardless of their exact form, the generalized abundance-occupancy relationships documented here have potential to contribute to the development of effective conservation management strategies. Recently there has been a growing interest in developing generalized, species-independent recovery frameworks and recovery targets (Hutchings and Kuparinen 2014; Westwood et al. 2014). The taxonomic abundance-occupancy relationships reported here can also be considered species-independent insofar as they do not typify the relationship for a single individual species but rather a broader taxonomic classification (e.g. birds, marine fishes, etc.). For example, a fundamental feature of one proposed species-independent target is carrying capacity (K) (Hutchings and Kuparinen 2014). If one had an estimate of K , an abundance-occupancy relationship could be used to estimate the area of habitat associated with the proportion of K used to inform decisions regarding the recovery target (Hutchings and Kuparinen 2014).

Using these species-independent relationships to predict abundance is a promising example of how such relationships could be valuable tools in developing generalized species recovery strategies (Gaston et al. 2006; Hui et al. 2009, 2012). Abundance is a fundamental parameter that plays an important role in understanding community structure

and species conservation. Thus, the provision of a primary correlate of abundance – particularly one that is related to habitat – can be informative when developing management and conservation strategies (Fisher and Frank 2004; ICES 2005). Although abundance can be an informative metric of population or species viability, provided the scale is not too fine or localized, obtaining direct measures can be logistically problematic and unduly time-consuming (He and Gaston 2000). Consequently, the development of accurate and time-efficient methods can be effective in enabling scientists, managers and policy-makers to optimize species conservation strategies.

Species-independent abundance-occupancy relationships, such as those documented here, might also provide informative tools in forecasting changes in abundance with change in habitat (He and Gaston 2000; Hui et al. 2009, 2012; Azaele et al. 2012). Generalized abundance-occupancy relationships could also serve as a first step in developing species-independent recovery strategies. In such cases, the species-independent relationships would serve as reference points for differentiating recovery strategies that are scientifically defensible versus those that might have been influenced by other factors.

Although species-independent abundance-occupancy relationships provide a foundation for some promising applications, it is important to stress that their primary utility may be to serve as ‘starting points’ and, like all models, will have inherent limitations and caveats. For instance, this approach would not be suitable for a species or population that has experience declines due to factors independent of habitat size, such as disease or invasive species. Additionally, it is likely that the taxonomic scale at which a taxonomic group exhibits a species-independent relationship will vary from taxon to

216 taxon. In order to further address this issue, future analyses should focus on increasing
217 the number of data points, in particular for groups with low sample sizes.

218 Spatially extensive evidence of a positive relationship among broad taxonomic
219 groupings is an empirically compelling finding that further underpins the strength and
220 depth of the abundance-occupancy relationship. In addition to furthering an
221 understanding of large-scale population dynamics, these relationships may prove integral
222 in the future development of time-sensitive, effective, and unbiased conservation
223 management practices, including species-independent recovery targets.

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References

- Azaele, S., Cornell, S.J., and Kunin, W.E. 2012. Downscaling species occupancy from coarse spatial scales. *Ecol. Appl.* **22**: 1004–1014. doi: 10.1890/11-0536.1.
- Blackburn, T.M., Cassey, P., and Gaston, K.J. 2006. Variations on a theme: Sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. *J. Anim. Ecol.* **75**: 1426–1439. doi: 10.1111/j.1365-2656.2006.01167.x.
- Blackburn, T.M., Gaston, K.J., Quinn, R.M., Arnold, H., and Gregory, R.D. 1997. Of mice and wrens : the relation between abundance and geographic range size in British mammals and birds. *Philos. Trans. R. Soc. Biol. Sci.* **352**: 419–427.
- Borregaard, M.K., and Rahbek, C. 2010. Causality of the relationship between geographic distribution and species abundance. *Q. Rev. Biol.* **85**: 3–25.
- Brown, J.H. 1984. On the relationship between abundance and distribution of species. *Am. Nat.* **124**: 255. doi: 10.1086/284267.
- COSEWIC. 2013. Instructions for the Preparation of COSEWIC Status Reports. 1–30. Available from http://www.cosewic.gc.ca/pdf/Instructions_e.pdf.
- Fisher, J., and Frank, K. 2004. Abundance-distribution relationships and conservation of exploited marine fishes. *Mar. Ecol. Prog. Ser.* **279**: 201–213. doi: 10.3354/meps279201.
- Gaston, K.J. 1996. The multiple forms of the interspecific abundance-distribution relationship. *Oikos*, **76**: 211–220.
- Gaston, K.J. 1997. Interspecific abundance-range size relationships: an appraisal of mechanisms. *J. Anim. Ecol.* **66**: 579–601.
- Gaston, K.J., Blackburn, T.M., Greenwood, J.J., Gregory, R.D., Quinn, R.M., and Lawton, J.H. 2000. Abundance-occupancy relationships. *J. Appl. Ecol.* **37**: 39–59. doi: 10.1046/j.1365-2664.2000.00485.x.
- Gaston, K.J., Blackburn, T.M., and Lawton, J.H. 1997. Interspecific abundance-range size relationships : an interspecific appraisal of mechanisms. *J. Anim. Ecol.* **66**: 579–601.
- Gaston, K.J., Borges, P.A. V, He, F., and Gaspar, C. 2006. Abundance, spatial variance and occupancy: arthropod species distribution in the Azores. *J. Anim. Ecol.* **75**: 646–56. doi: 10.1111/j.1365-2656.2006.01085.x.
- Gaston, K.J., and Curnutt, J.T. 1998. The dynamics of abundance-range size relationships. *Oikos*, **81**: 38–44.

- Gaston, K.J., and Fuller, R.A. 2009. The sizes of species' geographic ranges. *J. Appl. Ecol.* **46**: 1–9. doi: 10.1111/j.1365-2664.2008.01596.x.
- Gaston, K.J., and Lawton, J.H. 1990. Effects of scale on the relationship between regional distribution and local abundance. *Oikos*, **58**: 329–335.
- He, F., and Gaston, K.J. 2000. Estimating species abundance from occurrence. *Am. Nat.* **156**: 553–559.
- Hui, C., Boonzaaijer, C., and Boyero, L. 2012. Estimating changes in species abundance from occupancy and aggregation. *Basic Appl. Ecol.* **13**: 169–177. doi: 10.1016/j.baae.2012.02.003.
- Hui, C., McGeoch, M. a, Reyers, B., le Roux, P.C., Greve, M., and Chown, S.L. 2009. Extrapolating population size from the occupancy-abundance relationship and the scaling pattern of occupancy. *Ecol. Appl.* **19**: 2038–48. Available from <http://www.ncbi.nlm.nih.gov/pubmed/20014577>.
- Hui, C., and McGeoch, M.A. 2007. Capturing the “droopy-tail ” in the occupancy-abundance relationship. *Ecoscience*, **14**: 103–108.
- Hutchings, J.A., and Kuparinen, A. 2014. A generic target for species recovery. *Can. J. Zool.* **92**: 371–376.
- ICES. 2005. Report of the Working Group on Zooplankton Ecology (WGFE), 21-26 February 2005. Santander, Spain. Available from <http://brage.bibsys.no/xmlui/bitstream/handle/11250/100803/G05.pdf?sequence=1>.
- IUCN Standards and Petitions Subcommittee. 2014. Guidelines for using the IUCN red list categories and criteria. **Version 11**: Prepared by the Standards and Petitions Subcommitt. Available from <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>.
- R Core Team. 2014. R: A Language and Environment for Statistical Computing. R Found. Stat. Comput.: Vienna, Austria. Available from <http://www.r-project.org>.
- Webb, T.J., Noble, D., and Freckleton, R.P. 2007. Abundance-occupancy dynamics in a human dominated environment: linking interspecific and intraspecific trends in British farmland and woodland birds. *J. Anim. Ecol.* **76**: 123–34. doi: 10.1111/j.1365-2656.2006.01192.x.
- Westwood, A., Reuchlin-Hughenoltz, E., and Keith, D.M. 2014. Re-defining recovery: A generalized framework for assessing species recovery. *Biol. Conserv.* **172**: 155–162. Elsevier Ltd. doi: 10.1016/j.biocon.2014.02.031.

- Williamson, M., and Gaston, K. 1999. A simple transformation for sets of range sizes. *Ecography (Cop.)* **68**: 674–680.
- Williamson, M., and Gaston, K.J. 2005. The lognormal distribution is not an appropriate null hypothesis for the species-abundance distribution. *J. Anim. Ecol.* **74**: 409–422. doi: 10.1111/j.1365-2656.2005.00936.x.
- Zuckerberg, B., William, F., and Corwin, K. 2009. The consistency and stability of abundance – occupancy relationships in large-scale population dynamics. *J. Anim. Ecol.* **78**: 172–181. doi: 10.1111/j.1365-2656.2007.0.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York. doi: 10.1007/978-0-387-87458-6.

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Table 1. A summary of the 6 abundance-occupancy models tested, where the response variable (occupancy) is a function of combinations of predictors including both fixed (abundance and abundance²) and random effects (random intercept '1|Taxon' or random intercept and slope '1+Abundance|Taxon'). The best model following model selection was 2C and was hence used to extract taxon specific relationships as shown in Figure 2.

Model	Fixed Effects [Estimate (±SE)]		Random Effects	
	Abundance	Abundance ²	Term Included	Variance associated [*]
A	0.371 (0.06)**	-	-	-
B	0.328 (0.05)**	-	(1 Taxon)	0.467
C	0.355 (0.13)**	-	(1+Abundance Taxon)	0.540
2A	0.560 (0.23)**	-0.023 (0.03)	-	-
2B	0.888 (0.17)**	-0.069 (0.02)**	(1 Taxon)	0.473
2C	1.016 (0.20)**	-0.086 (0.03)**	(1+Abundance Taxon)	0.436

* The proportion of total variance in model associated to the random effect structures (i.e. random intercept or random intercept and slope).

** Significant predictor variable.

Figures Captions

Fig. 1. Linear regression between occupancy and abundance for all data points. (Regression equation: $y = 0.37x + 0.84$; $r^2 = 0.07$, $n=477$, F-test for the significance of the slope: $p<0.0001$)

Fig. 2. Relationship between occupancy and abundance for endangered species in Canada, by taxonomic group. (n =number of data points, s =number of species). The lines represent model fits to the data from the final model 2C.

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