

Intra-specific abundance-distribution relationships

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Mechanisms that have been proposed to explain the relationship between abundance (mean abundance at occupied sites) and distribution (proportion of sites occupied) have been based on (1) differences among species that affect either their ability to exploit resources or their ability to move through the landscape, (2) differences in species' landscapes that affect rates of successful dispersal of individuals, or (3) statistical arguments. Existence of an intra-specific abundance-distribution relationship where species differences cannot be a factor would provide evidence that differences in species' landscapes likely contribute to the inter-specific abundance-distribution relationship. We examined the intra-specific relationship between abundance and distribution for 20 species of boreal forest songbirds. Abundance and distribution were calculated for each species in 52 to 119 locations over an area of 300 km × 100 km of northwestern Ontario. Based on separate regressions, 16 of the species demonstrated significant positive relationships between abundance and distribution at $\alpha = 0.05$. The weighted mean partial correlation for all species combined was greater than zero ($P < 0.05$). Meta-analysis indicated that there is no significant variation in the abundance-distribution correlation among species. This study provides evidence that amount of habitat within a landscape contributes to a positive intra-specific abundance-distribution relationship and therefore suggests that this factor could also contribute to the positive abundance-distribution relationship that is commonly found among species within an assemblage.

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A positive relationship between abundance and distribution of species within a taxonomically related assemblage has been well documented in the literature (see Brown 1984, Gaston and Lawton 1990, Hanski et al. 1993, Gaston 1994 for review) but for a few exceptions (Gaston and Lawton 1990). Mechanisms that have been proposed to explain the relationship between abundance (mean abundance at occupied sites) and distribution (proportion of sites occupied) have been based on (1) differences among species that affect their abilities to exploit resources (ecological specialization hypothesis; Brown 1984), (2) differences among species in their abilities to move through the landscape (metapopulation hypothesis; Gyllenberg and Hanski 1992), (3) differences in the amount of habitat among species'

landscapes (Gyllenberg and Hanski 1992, Venier and Fahrig 1996) or, (4) a statistical argument that random or clumped distributions of individuals among sites will result in the observed phenomenon (Wright 1991).

The ecological specialization hypothesis (Brown 1984) argues that species that can exploit a large number of different resources locally will have high local densities (generalists) due to increased survivorship and reproduction. These species will also be able to survive in many places because there should on average be more places that have sufficient resources and they will therefore occur over large areas. Conversely, those species that can exploit only a few resources (specialists) will be neither locally abundant nor widely distributed. Therefore in a species assemblage where there is varia-

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tion in the level of ecological specialization, a positive relationship between distribution and abundance is expected.

The metapopulation hypothesis (Gyllenberg and Hanski 1992) predicts a positive relationship between the local abundance at occupied sites and the fraction of sites occupied (distribution), given an assemblage of species with variation in (1) dispersal rate in relation to intrinsic growth rate, (2) probability of a disperser finding a patch before dying or (3) extinction rate in relation to rate of successful colonization. These predictions are based on a structured metapopulation model in which local population size is affected by dispersal between patches as well as by dynamics within patches. The metapopulation hypothesis argues that any characteristics that vary among species and can create differences in the rate of successful dispersal will generate a positive abundance-distribution relationship.

Venier and Fahrig (1996) argue that the most likely characteristic to generate differences in disperser success is the total area of habitat in the landscape available to the species. On a single landscape, each species of an assemblage perceives the habitat composition differently depending on habitat preferences. Therefore different amounts of habitat are available to the different species. Most landscapes consist of many types of habitat in different amounts. Those species that use a higher percentage of the landscape, by using more common habitat types or more habitat types, are expected to be both more abundant and more widely distributed because of an increased rate of successful dispersal. Dispersal is more likely to be successful when there is more habitat available to disperse to. The idea that species that can use more habitat will have more successful dispersal on average and therefore will be more abundant should not be confused with the ecological specialization argument. The ecological specialization hypothesis relies on the effect of amount of local resources on local populations whereas the habitat-amount argument relies on the influence of amount of regional habitat on local populations.

The influence of amount of habitat in the landscape relies on the same mechanism, that of dispersal success, as the metapopulation hypothesis. However the attribute responsible for variation in dispersal success is explicitly the amount of habitat on the landscape available to the species. Habitat outside the area being sampled is expected to influence the abundance inside the area being sampled through dispersal.

Wright (1991) argued that if species have a random or clumped spatial distribution and some are more abundant than others then the relationship between abundance and distribution will be positive. Within species, if the distribution of individuals is random, then no biological explanation is necessary; hence this has been called the null hypothesis. A clumped or negative binomial distribution is the common distribu-

tion for animal populations (Taylor et al. 1978, Wright 1991) and requires a biological explanation for this clumping. However, Wright's hypothesis does not actually suggest any biological mechanism for the observed distributions. It is this mechanism that we examine in this paper.

These hypotheses were all proposed to explain a positive relationship between distribution and abundance for an assemblage of species. Mechanisms that rely on variation in amount of habitat in the landscape also predict a positive *intra*-specific abundance-distribution relationship where abundance and distribution of a single species are measured in different landscapes containing different amounts of habitat. This is not a prediction of the ecological specialization hypothesis, which relies on variation between species in the degree of ecological specialization. For a single species there is little or no variation in specialization; therefore, this hypothesis cannot predict an *intra*-specific relationship. The metapopulation hypothesis addresses this relationship indirectly. A positive *intra*-specific relationship cannot be accounted for through differences between species in their movement abilities, but as we have argued, variation in amount of habitat on the landscape can generate variation in dispersal success. A single species in different regions will experience variation in landscape composition and configuration. If metapopulation dynamics are operating through variation in amount of habitat on the landscape then we predict a positive *intra*-specific relationship.

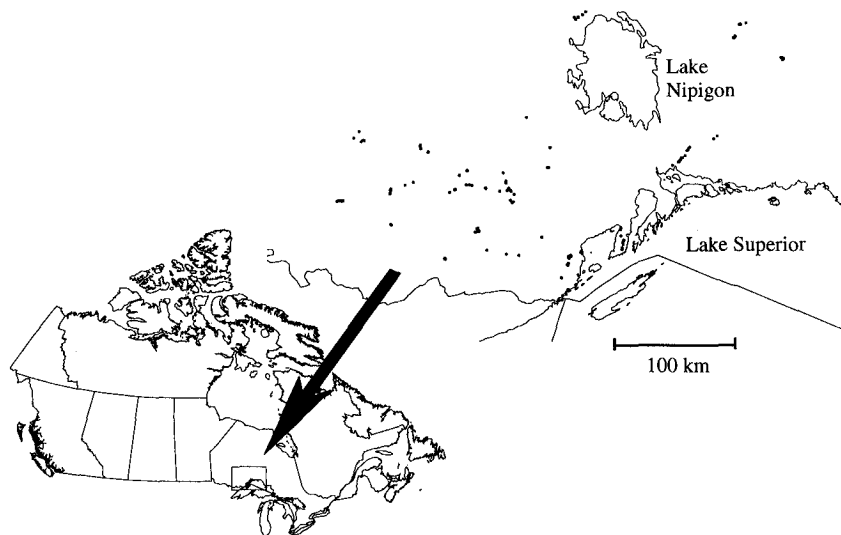
We tested the prediction of a positive *intra*-specific relationship between abundance and distribution for each of twenty species of boreal forest songbirds in northwestern Ontario, Canada. A positive *intra*-specific relationship would support the idea that variation in amount of habitat on the landscape influences the metapopulation dynamics of species to generate a positive relationship over a number of different landscapes. This landscape variation could also account at least in part for a positive *inter*-specific abundance-distribution relationship on a single landscape for the reasons outlined above and in Venier and Fahrig (1996).

Methods

Study area and site selection

As part of an ongoing research program at the Canadian Wildlife Service, Environment Canada, bird census, vegetation and global positioning data were collected in 131 landscapes in an area of approximately 300 km × 100 km throughout northwestern Ontario in 1989 and 1991. The sampling points ranged from 48.18° N, 89.49° W to 50.28° N, 88.87° W (south to north) and 48.91° N, 91.83° W to 49.81° N, 86.62° W (west to east) (Fig. 1). Five sample points (sites) were located in

Fig. 1. Landscape locations in Northwestern Ontario, Canada.



each landscape and were on average approximately 300 m apart and at least 100 m from the road. We use the term landscape to indicate an area of influence around a local site which is at a larger scale than the local sample for the organism. The sites of a landscape were in a circle or a line. Landscapes were selected to obtain samples of all vegetation types. Selection was limited by accessibility of forest landscapes and rarity of some types. Initial selection of the landscapes was conducted using Forest Resource Inventory Maps, a system of forest (timber) inventory carried out by the Ontario Ministry of Natural Resources and based mainly on aerial photograph interpretation and some ground truthing (Gillis and Leckie 1993).

Geographic position (latitude and longitude) was determined at most sites within all landscapes using a Garmin Survey II Global Positioning System with differential correction (accuracy of 1–3 m). The position of the most central site of the landscape where data were available was used as the position of the landscape. If no site was more central than any others the third site was chosen.

Bird counts

Bird census data were collected using a point count method (Welsh 1995). Each site was visited twice by the same observer, once in early to mid-June and once in mid- to late June between sunrise and 10.00. Observers conducted 10-min counts at each site for each visit. All birds seen or heard were recorded. The larger of the counts from the two visits was used as the estimate of abundance for each site and territorial, singing males were recorded as two individuals (Welsh 1995). Abundance for a landscape was calculated as the mean abundance in occupied sites of the landscape. Distribu-

tion was measured as the maximum number of sites occupied in the landscape.

Vegetation

The vegetation type of each site was described according to the Forest Ecosystem Classification (FEC) of Northwestern Ontario (Sims et al. 1989). The FEC is a classification of the common, mature (over 50 yr of age) vegetation associations of northwestern Ontario which describes 38 separate vegetation types. A classification key is used to identify the vegetation type of a 10 m × 10 m plot. Five of these plots were keyed out at each site for vegetation type, one at the centre of the site and one at each plot 50 m from the centre of the site directly north, south, east and west. The mode of the vegetation types for the 25 plots (5 sites) was used to characterize the vegetation type of the landscape.

Statistical analyses

The 20 species of forest songbirds that occurred in at least 50 landscapes were examined for an intra-specific relationship between abundance and distribution. We examined the distribution of individuals at sites for each species by calculating the index of dispersion (I) (Pielou 1974) where

$$I = \frac{\sum (x - \bar{x})^2}{\bar{x}}$$

and computing the statistic

$$T = \sqrt{[2I]} - \sqrt{[2n - 1]},$$

where n is the number of samples. This test statistic falls between -1.96 and $+1.96$ 95% of the time when the abundance is randomly distributed. Species with distributions that were not distinguishable from random should be removed from the analysis because a positive abundance-distribution relationship does not require a mechanistic explanation (Wright 1991).

Multiple regression (SAS Institute 1988) was performed with log (mean abundance at occupied sites + 1) as the response variable and with vegetation type, latitude, longitude, second order latitude, second order longitude and distribution as explanatory variables. Vegetation type was entered as a class variable to control for a potentially spurious positive relationship. Both abundance and distribution will be similarly affected by vegetation type. A station that is composed of good habitat is more likely to be occupied and to have higher abundance. The quality of habitat is expected to be spatially autocorrelated. If there are good quality landscapes which should on average have high distribution and high abundance and bad quality landscapes with low distribution and low abundance then there will be a positive relationship between distribution and abundance due to the differences in habitat quality between landscapes and the fact that habitat tends to be of the same quality within landscapes. Habitat type was included to remove this possible effect.

Populations at the edge of a species range typically have low abundance and distribution (See Brown 1984 for examples), while those at the centre of the range have high abundance and distribution. To control for this possible effect, we included the geographic position of the site in the statistical models relating abundance to distribution. In this way, any variation in abundance that is due to the geographic position is removed before examining the remaining relationship with distribution. By including both latitude and longitude in the model we can fully describe the two-dimensional space. By including the second order terms we can model the change in abundance of the species regardless of where the centre of the range is. Latitude and longitude are spherical co-ordinates and therefore the length of a degree longitude changes with latitude; however, the error introduced is very small.

We examined the Type III Mean Square of distribution to determine if there was a relationship between distribution and abundance after controlling for the effects of vegetation type and geographic location. We conducted a separate regression analysis for each species. The sample size for each species depended on the number of landscapes where the species was found, and ranged from 52 to 119.

We combined the results of the 20 analyses into a single meta-analysis (Hunter and Schmidt 1990), using the partial r_i value for the distribution variable as the effect size for each species i . The objective of the meta-analysis was to determine the amount of variance

in the estimates of the effect size. If the variance among species' effect sizes is not different from zero then the overall weighted r value for all species combined ($\Sigma [N_i r_i] / \Sigma N_i$) (Hunter and Schmidt 1990: 100) can be used as the population correlation coefficient, where N_i is the number of observations (landscapes) for species i . The meta-analysis assumes that the variance of the population correlations can be calculated as the variance of observed correlations minus the sampling error. The variance of the observed correlations is estimated as

$$s_r^2 = \frac{\Sigma (N_i (r_i - \bar{r})^2)}{\Sigma N_i}$$

And the sampling error is calculated as

$$\sigma_e^2 = (1 - \bar{r}^2)^2 / (N - 1).$$

The r_i values were calculated as the square root of the Type III regression sums of squares for (Hunter and Schmidt 1990) distribution over the total sums of squares for the model. We calculated a 95% confidence interval around the weighted r value based on the overall sample size to determine if the overall correlation was different from zero (Zar 1984).

Results

For all 20 species we rejected the null hypothesis of a Poisson distribution (Table 1); therefore, all species were included in the analysis. Sixteen species showed a significant positive relationship between distribution and abundance at the $\alpha = 0.05$ level (Table 2). All 20 slope estimates were positive (Table 2). The residuals from all models were examined and fit the assumptions of linear regression.

The meta-analysis using the partial r_i for distribution as the effect size (Table 2) indicated that the weighted average r was $+0.261$. The total sample size was 1651 and the average sample size was 82.6. The sample variance was 0.00933 and the sampling error variance was 0.0107; therefore, the population correlation variance was -0.001 which strongly indicates that there are no demonstrable differences in the effect sizes (r_i) among species (Hunter and Schmidt 1990: 109). A negative correlation variance is not unexpected in a meta-analysis because the population correlation variance is calculated as the difference between the variance of observed correlations (which is a sample estimate) and the statistically given sampling error variance. There will be some error in the sample estimate and therefore when the correlation variance is zero the error will cause the estimate to be negative about half the time (Hunter and Schmidt 1990). The lower limit of the

Table 1. Index of dispersion and the normally distributed dispersion statistic for each of 20 species. The null hypothesis is a Poisson distribution of abundance at sites. The null hypothesis is rejected in all species.

Species common name	Scientific name	<i>N</i>	<i>I</i>	$\sqrt{(2I)} - \sqrt{(2n-1)}$
American robin	<i>Turdus migratorius</i>	335	555	7.44
Blackburnian warbler	<i>Dendroica fusca</i>	350	620	8.78
Black-throated green warbler	<i>Dendroica virens</i>	315	556	8.25
Chipping sparrow	<i>Spizella passerina</i>	355	718	11.28
Dark-eyed junco	<i>Junco hyemalis</i>	260	516	9.35
Golden-crowned kinglet	<i>Regulus satrapa</i>	500	839	9.36
Hermit thrush	<i>Catharus guttatus</i>	420	899	13.43
Least flycatcher	<i>Empidonax minimus</i>	395	1221	21.38
Magnolia warbler	<i>Dendroica magnolia</i>	395	740	10.38
Nashville warbler	<i>Vermivora ruficapilla</i>	560	1391	19.29
Ovenbird	<i>Seiurus aurocapillus</i>	505	840	9.23
Red-breasted nuthatch	<i>Sitta canadensis</i>	355	529	5.91
Red-eyed vireo	<i>Vireo olivaceus</i>	330	612	9.33
Ruby-crowned kinglet	<i>Regulus calendula</i>	450	780	9.50
Swainson's thrush	<i>Catharus ustulatus</i>	510	1010	13.02
Tennessee warbler	<i>Vermivora peregrina</i>	350	979	17.81
White-throated sparrow	<i>Zonotrichia albicollis</i>	595	1277	16.05
Winter wren	<i>Troglodytes troglodytes</i>	515	841	8.93
Yellow-bellied flycatcher	<i>Empidonax flaviventris</i>	295	505	7.51
Yellow-rumped warbler	<i>Dendroica coronata</i>	550	816	7.26

95% confidence limit on ρ was 0.216 and the upper limit was 0.305 suggesting that there is an overall positive relationship between abundance and distribution.

Discussion

Our results provide strong evidence for a positive intra-specific abundance-distribution relationship. This relationship was predicted by the habitat availability hypothesis for the inter-specific abundance-distribution relationship (Venier and Fahrig 1996). Our results therefore provide tentative support for this hypothesis. At a minimum they suggest that differences among landscapes (as opposed to differences among species) are at least partly responsible for the abundance-distribution relationship. Hypotheses that rely directly on differences between species (Gyllenberg and Hanski 1992), such as dispersal ability or differences in ecological specialization (Brown 1984), would not predict a positive intra-specific relationship under the conditions of this study. By examining the intra-specific relationship we have effectively controlled for differences among species. We have also examined and rejected the possibility that the positive relationship is a function of a random distribution of individuals by establishing that the distributions of individuals within species are not random. The distributions of species are clumped and therefore require explanation. Many possible factors could lead to clumped distributions and we cannot eliminate every possible factor that may cause clumping. Our results offer evidence that is suggestive of a habitat-amount effect because the only attributes that vary from sample to sample are landscape related ones.

We argued previously that for a species assemblage each species perceives the landscape differently depending on its own specific habitat usage and therefore in a single location there is variation among species in the amount of habitat on the landscape (Venier and Fahrig 1996).

Results from simulation experiments (Venier and Fahrig 1996) indicate that differences in amount of breeding habitat for species within a landscape can account for a positive relationship between distribution and abundance of species. Populations in simulated landscapes with more breeding habitat reach a higher mean abundance level and a greater distribution and do so more quickly than populations in landscapes with less breeding habitat. More breeding habitat makes successful dispersal much more likely. Successful dispersal has been shown to increase the size of small populations in several empirical studies (Connor et al. 1983, Rey and Strong 1983, Fahrig and Merriam 1985). Similarly, successful dispersal to unoccupied patches will increase the distribution of the species. Therefore, we expect a positive abundance-distribution relationship when there is variation in amount of habitat.

The two most commonly cited hypotheses to explain the positive inter-specific distribution-abundance relationship use either the variation in the level of ecological specialization (Brown 1984) or movement within metapopulations (Gyllenberg and Hanski 1992). The ecological specialization hypothesis (Brown 1984) relies on between-species variation in ecological specialization of which there is none in the intra-specific case. Therefore, the existence of an intra-specific relationship between distribution and abundance cannot be predicted from Brown's hypothesis. This does not suggest that the ecological specialization mechanism is not operating

Table 2. Sample sizes and statistics from multiple regression models for each of 20 species of forest songbirds. The response variable for all models is $\log(\text{abundance}+1)$. The independent variables are Distribution, Latitude, Longitude, Latitude², Longitude², and Vegetation Type. Partial r_i values are for the Distribution variable. N is the number of observations for each species.

Species name	N	Distribution MS Type III	Distribution F	Distribution P	Partial r	Slope estimate
American robin	67	0.286	9.44	0.004	0.33	+0.35
Blackburnian warbler	70	0.205	4.59	0.038	0.27	+0.28
Black-throated green warbler	63	0.297	6.42	0.016	0.30	+0.33
Chipping sparrow	71	0.518	16.44	0.000	0.42	+0.48
Dark-eyed junco	52	0.311	11.95	0.001	0.38	+0.48
Golden-crowned kinglet	100	0.147	6.90	0.011	0.23	+0.22
Hermit thrush	84	0.304	7.25	0.010	0.24	+0.34
Least flycatcher	79	1.023	12.55	0.001	0.34	+0.42
Magnolia warbler	62	0.001	0.06	0.811	0.03	+0.02
Nashville warbler	112	1.028	31.30	0.000	0.35	+0.44
Ovenbird	101	0.357	9.76	0.003	0.18	+0.39
Red-breasted nuthatch	71	0.022	2.46	0.125	0.18	+0.10
Red-eyed vireo	90	0.856	21.56	0.000	0.33	+0.59
Ruby-crowned kinglet	66	0.303	10.16	0.003	0.29	+0.42
Swainson's thrush	102	0.766	15.50	0.000	0.31	+0.45
Tennessee warbler	70	0.312	4.33	0.044	0.18	+0.47
White-throated sparrow	119	1.110	19.51	0.000	0.38	+0.41
Winter wren	103	0.139	4.35	0.041	0.20	+0.18
Yellow-bellied flycatcher	59	0.017	0.98	0.330	0.09	+0.11
Yellow-rumped warbler	110	0.088	2.81	0.098	0.14	+0.14

but it does suggest that other mechanisms are operating.

The results of this study provide support for the second and third parts of the metapopulation hypothesis (Gyllenberg and Hanski 1992). Variation in the probability of a disperser finding a patch before dying or extinction rate in relation to rate of successful colonization can be due to variation in amount of habitat on the landscape. The first part of this hypothesis could still be operating but would not predict the intra-specific abundance-distribution relationship. In addition, differences between species that caused variation between species in disperser success would not generate a prediction of an intra-specific relationship. Nee et al. (1991) suggested another hypothesis related to metapopulation dynamics that has been called the 'carrying capacity hypothesis' (Gaston et al. 1997). They suggested that different species in an assemblage would have different local carrying capacities. Larger local populations would be less likely to go extinct and will have higher colonization rates than smaller ones. Therefore, locally more abundant species will occupy more patches at equilibrium. In the intra-specific case, different local sites are required to have different local carrying capacities for a single species. In our analysis we have included habitat as an explanatory variable which should remove any effect of differences in local carrying capacity.

To our knowledge, only one other study has tested for and found an intra-specific relationship between *independent* measures of distribution and abundance (Hanski et al. 1995). The intra-specific relationship between abundance and distribution has been examined in the past but almost always in the context of using distribution (proportion of sites occupied) to estimate abundance (Gerrard and Chiang 1970, Wilson and Room 1983, Ward et al. 1986, Bart and Klosiewski 1989, Robbins et al. 1989, Hergstrom and Niall 1990). Positive relationships have always been found but the results are confounded because abundance was calculated across all sites including empty ones. Abundance measured in this way is necessarily related to distribution because both measures are influenced the same way by empty sites.

The size of the landscape on which a study is conducted is important in determining the potential influence of amount of habitat on abundance and distribution. The mean abundance of occupied sites is measured at the scale of an individual site. The amount of habitat around that site is expected to influence the abundance at that site. However, distribution is measured at the scale of the landscape. The size of the landscape on which abundance and distribution are measured is an arbitrarily defined area but the area that potentially influences abundance and distribution is not. It could be argued that the scale of landscapes in the study is too small to represent true metapopulations

for forest birds. However, the mechanism proposed here does not require a metapopulation to operate. It is only necessary to have sampling sites that can contain more than one pair of birds and dispersal that can result in the occupation of a sampling site by a new or additional pair. Our landscapes in this study meet these criteria.

For the mechanism of disperser success to influence both abundance and distribution through amount of habitat, the sampled landscape must be similar or smaller in scale to the dispersal distance of the organisms. Habitat outside the dispersal distance of an organism will have much less influence over the abundance and distribution than habitat within the dispersal distance. Dispersal distances for forest songbirds are not well known due to very low recapture rates of less than 10% (Villard et al. 1995); therefore, the fate of most juveniles is unknown. For those recaptured, the median dispersal distance is often close to or less than 1 km (for example, *Cinclus cinclus*, 3000–5000 m, Tyler et al. 1990; *Ficedula albicollis*, 518–840 m, Pärt 1990, *F. hypoleuca*, 500–3000 m, Nyholm 1986; *Hirundo rustica*, 6375 m, Sheilds 1984; *Melospiza melodia*, 90–120 m, Arcese 1989; *Parus atricapillus*, 198–1110 m, Weise and Meyer 1979; *Parus major*, 600–100 m, van Tienderen and van Noordwijk 1988; *Passerina cyanea*, 500–900 m, Payne 1991; *Sitta europaea*, 800–1120 m, Matthysen and Schmidt 1987).

The existence of a positive intra-specific abundance-distribution relationship is consistent with the idea that variation in amount of habitat on the landscape can generate a positive abundance-distribution relationship but it is not a direct test of the idea. A direct test would require an examination of the relationship between the amount of habitat on the landscape and both the abundance and distribution. Habitat can be of different qualities depending on its ability to supply the necessary resources for reproduction and survival, so the area of habitat on the landscape would have to be weighted by its quality. This weighting would be different for each species in the inter-specific case.

Given the ubiquity of the relationship between abundance and distribution, it is likely that different mechanisms are responsible for the relationship under different conditions. However, the positive intra-specific relationship that we found overall argues for the influence of amount of habitat on the landscape on the relationship. This would also be true for different species in the same landscape since the realized habitat of the landscape depends on the species' interaction with it.

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