The Combined Influence of the Local Environment and Regional Enrichment on Bird Species Richness

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ABSTRACT: It is generally accepted that local species richness at a site reflects the combined influence of local and regional processes. However, most empirical studies evaluate the influence of either local environmental variables or regional enrichment but not both simultaneously. Here we demonstrate the importance of combining these processes to understand continental scale richness patterns in breeding birds. We show that neither regional enrichment nor the local environment in isolation is sufficient to characterize observed patterns of species richness. Combining both sets of variables into a single model results in improved model fit and the removal of residual spatial autocorrelation. At short time scales local processes are most important for determining local richness, but as the time scale of analysis increases regional enrichment becomes increasingly important. These results emphasize the need for increased integration of multiple scales of processes into models of species richness.

Ecologists have long debated whether the richness of local communities is limited primarily by local factors such as the availability of niches (MacArthur 1964; Tilman 2004) or resources (Brown 1981; Wright 1983), or alternatively whether local richness is determined by the richness of the regional pool and thus more strongly related to regional scale variables that reflect evolutionary history and colonization dynamics (Ricklefs 1987; Ricklefs 2007). Local processes hypothesized to limit richness include competition for limited resources (Brown 1981), limited niche space (MacArthur 1964), and limiting similarity (Tilman 2004), all of which make it more difficult for species to persist at sites where large numbers of species already occur. An alternative explanation, based on the observation that local sites do not appear to be saturated with species (Ricklefs 1987; Stohlgren et al. 2008), suggests that local species richness is actually limited by the availability of species to colonize the site from the regional pool (Cornell and Lawton 1992; Harrison and Cornell 2008). While the specifics of exactly how regional richness translates into local richness have been poorly explored, it has been proposed that this may happen through a simple, neutral, colonization-extinction equilibrium (He et al. 2005). Under this scenario, local richness is expected to be more strongly tied to processes and events operating beyond the scale of the local community, such as diversification rates and biogeographic history (Ricklefs 1987; Ricklefs 2007).

Interestingly, most analyses of local scale species richness patterns analyze either the effects of the local environment (e.g., Gough et al. 2000; Kaspari et al. 2000) or the effects of regional richness (e.g., Karlson et al. 2004; Witman et al. 2004), despite suggestions that both sets of processes are important (Kaspari et al. 2000; Ricklefs 2000; Harrison and Cornell 2008). Only a small fraction of richness studies have actually examined the joint influence of local and regional factors on local species richness (e.g., Angermeier and Winston 1998; Griffiths 1999; Freestone

and Harrison 2006; Harrison et al. 2006; Qian et al. 2007; Hortal et al. 2008), leading to calls for

greater integration of local and regional influences into richness models (Harrison and Cornell

2008). Furthermore, in studies where both local environmental factors and regional richness have

been included in a single analysis, the analyses are typically used to confirm that both processes

are operating or to argue that one of the processes is important even after controlling for the other

(Cornell and Karlson 1996; Angermeier and Winston 1998; Karlson and Cornell 1999; Freestone

and Harrison 2006). This is an important step towards integrating the contributions of the two

scales of process, but stops short of providing information about the relative importance of local

and regional influences and how they interact to determine local diversity.

Determining the relative importance of local factors and regional enrichment represents an

important step towards a general understanding of the processes governing species richness

(Angermeier and Winston 1998; Griffiths 1999; Ricklefs 2000). If either the local environment

or regional enrichment dominates observed richness patterns then processes operating at that

scale will be the key to understanding diversity. However, if both scales contribute substantially

to observed richness patterns, then it may be necessary to explicitly consider both environmental

contributions and regional enrichment in models and empirical studies of species richness

(Harrison et al. 2006; Harrison and Cornell 2008). Variance partitioning provides a tool for

ascertaining the relative contributions of these two scales of processes. It determines how much

of the overall variance in local species richness can be uniquely ascribed to local environmental

variables and regional richness, and how much of the variance is explained by some combination

of the two categories of variables, but cannot be uniquely ascribed to either (Legendre and

Legendre 1998). As such it provides a valuable, but underutilized tool for understanding the

determinants of species richness. A pair of recent papers has partitioned the explained variance

between a categorical region factor and the local environment (Qian et al. 2007; Hortal et al. 2008), but we know of only one study to have used variance partitioning to evaluate the relative contributions of regional enrichment and local environmental variables (Harrison et al. 2006).

Here we show that for North American breeding birds both the local environment and regional enrichment contribute substantially to observed variation in species richness and use variance partitioning to the explore the relative importance of these two scales of processes. We start by establishing that both local environmental variables and regional richness are correlated with local richness and show that looking at only one of these categories of variables misses significant patterns in local richness. Variance partitioning analyses indicate approximately equal contributions of the two sets of variables at longer time scales (i.e., 10 years). Further, we establish the presence of collinearity between the two categories of predictor variables and illustrate its influence on conclusions drawn from analyzing only one category at time. Finally, we evaluate the influence of the time-scale of analysis on the variance partitioning results, and use the information gained from this analysis to explore possible ways in which local and regional influences combine to govern local species richness.

Methods

Data on local scale species richness were taken from the North American Breeding Bird Survey (Sauer et al. 2007)(BBS; Sauer et al. 2007). The BBS is a coordinated continental scale survey of bird diversity and abundance conducted once each year during the breeding season, typically in June. Each survey is conducted along a 40 km route, with stops every 800 m. At each stop a single observer conducts a three minute point count where all detected individuals are identified to species and tallied. Groups not well sampled using BBS methods including water birds, nocturnal birds, and raptors were excluded from analyses. As such, we focus on 305 land

bird species for analysis. In addition we only used routes that were judged to be quality routes by

the BBS coordinator (i.e., run type = 1). To minimize the potential underestimation of local

richness due to sampling effects, we calculated the average number of species observed over all

possible five year windows from 1997-2006 (see McGill 2003). While it has been suggested that

observed values of species richness may be biased due to differences in detection probabilities

(Nichols et al. 1998), the methods proposed for addressing this potential bias in BBS data are

based on unrealistic assumptions regarding the homogeneity of BBS routes (e.g., see Boulinier

et al. 1998) and analyses evaluating broad scale richness patterns based on observed richness and

estimated richness find almost identical results (Evans et al. 2008). Therefore we utilize observed

species richness values in this study.

For each of the 871 routes surveyed every year during this time span (Appendix A) we

characterized six local scale environmental variables within a 40km radius of the route's starting

coordinates, a scale that ensures the inclusion of the entire route. Data on mean summer

(June-August) and winter (December-February) temperatures and annual precipitation were

obtained from the Climatic Research Unit (http://www.cru.uea.ac.uk/cru/data/tmc.htm), and are

long term averages from 1961-1990 at 10' resolution. Summer and winter values of the

normalized difference vegetation index (NDVI; a remotely sensed measure of greenness) were

derived from the NASA Pathfinder AVHRR satellite at 8 km base resolution (average values

from 1982-2000 excluding 1994). NDVI is well correlated with measures of productivity and

standing green biomass (Chong et al. 1993; Paruelo et al. 1997) and is used here as a measure of

productivity. We characterized the mean elevation of each site using a 30-arc second digital

elevation model of North America

(http://edc.usgs.gov/products/elevation/gtopo30/README.html). Mean elevation is highly

correlated with a number of measures of elevational heterogeneity and was chosen out of these

measures because it yields the strongest correlations with richness. This suite of environmental

variables was chosen because the data are readily available at local grains and continental extents

and because measures of productivity (including NDVI) are known to be the primary correlates

of species richness in bird communities evaluated at this combination of grain and extent in

North America (Hurlbert and Haskell 2003; Currie et al. 2004) and at continental extents in

general (Hawkins et al. 2003a; Hawkins et al. 2003b). We used long-term average data to

facilitate the cross time-scale analyses. Due to issues with data availability, the temporal spans of

the biological data and environmental data overlap only partially or not at all. However, any

differences from the long term averages will be small compared to the continental variation in

these variables which is of interest.

     The richness of the regional species pool for each BBS survey was determined by overlaying

the range maps for all species included in the study, and counting the number of maps that

overlapped each local survey location. Range map data represent independent assessments of

species distributions based on expert opinion and were provided by NatureServe (Ridgely et al.

2000). This approach could potentially include species in the pool that cannot use the particular

habitat present at the site (Srivastava 1999), but we follow Ricklefs' (2000) recommendation that

this is the most appropriate approach to defining the regional pool.

     Three types of regression models were used to explain variation in local species richness. In

the Local Environment model all six local environmental variables were used as predictors. In

the Regional Enrichment model, regional richness was the sole predictor. The Combined model

included both sets of predictor variables. In all models, quadratic terms were included for each

variable to account for potential non-linear relationships. Half of the routes were randomly

selected to fit the regression models and the other half of the routes were used to evaluate their performance. Variance partitioning analyses were conducted using standard methods based on the results of these three regression models (Legendre and Legendre 1998). Because values of species richness are reasonably large we treat them as continuous data (as is common practice; e.g., Hawkins et al. 2003a; Rahbek et al. 2007) instead of explicitly incorporating discrete error structure (as is also commonly done e.g., Schweiger et al. 2007). The performance of the three models was compared using AIC_c (Burnham and Anderson 2002).

In addition to the multiple regressions we conducted a path analysis to examine the causal relationships between these factors and the regional environment, which we defined as the same suite of environmental variables measured within a 320 km radius of the starting coordinates. Results were qualitatively similar using regional scales with radii ranging from 160-640 km. We also evaluated patterns of spatial autocorrelation in the residuals of the models using Moran's I (Legendre and Legendre 1998). In calculating Moran's I, we grouped all pairwise comparisons of BBS routes into 25 distance classes, each containing the same number of comparisons. The confidence intervals are based on a Bonferroni-corrected significance level of 0.002.

We also evaluated the effect of time-scale on the variance partitioning analysis by using windows from 1 to 10 years to estimate species richness. For each time scale we calculated the mean cumulative local richness of all possible contiguous samples of the appropriate length occurring between 1997 and 2006 (see White 2004). These mean richness values were then analyzed as described above for each different time-span. The ten year time span represents a compromise between having a long enough time span to evaluate time scale effects and having enough continuously sampled routes to provide a good coverage of the sampled regions.

Results and Discussion

Analyzing local and regional determinants separately and simultaneously

Within this single dataset we observe two common patterns of species richness: 1) a positive relationship between local and regional richness (fig. 1a; $r = 0.56$); and 2) a strong relationship between a suite of local environmental variables and local richness, where the primary correlation is with an estimate of productivity (fig. 1c; $r_{NDVI,summer} = 0.68$). The majority of studies investigating patterns of species richness examine only one of these two types of relationships, and the presence of a strong correlation has been taken (implicitly or explicitly) as evidence for that variable or suite of variables as an important determinant of observed geographic patterns (e.g., Kaspari et al. 2000; Allen et al. 2002; Karlson et al. 2004; Witman et al. 2004). However, when we look at either pattern in more detail we see a significant signal of the other set of variables on species richness. The simple regional richness model significantly underestimates species richness in communities with high NDVI and overestimates richness in communities with low NDVI (fig. 1a-b). The equivalent pattern is seen in the local environment model, which underestimates richness when the regional pool is species rich, and overestimates it where the regional pool is species poor (fig. 1c-d). Because both sets of variables have an important influence on local richness, including both improves the overall fit of the model (fig. 1e-f), with the combined model clearly favored in AIC comparisons (ΔAIC_c for the Local Environment model = 162.0; Regional Enrichment model = 290.3; Combined model = 0; ΔAIC_c values > 10 are considered to represent almost no support for the model). These results are similar to those of Harrison et al. (2006), which indicate that both local environmental factors and regional richness influence the local richness of serpentine floras in California. However, in contrast to Harrison et al.'s results (see also Harrison and Cornell 2008) our analysis suggests that productivity is directly related to richness at the local scale (fig. 1; Appendix A).

If the contributions of local environment and regional richness were independent of one another then while a combined analysis would produce a model with greater explanatory power, conclusions regarding the importance of either factor based on analyzing it in isolation would be unaffected. However, our results suggest collinearity between regional richness and the local environmental variables (all environmental variables are correlated with regional richness; P-values < 0.005) leading to a substantial fraction of variation that cannot be uniquely ascribed to either local or regional processes (fig. 1f). Had we analyzed either the local environment or regional richness alone, we would have ascribed this non-unique variance to the variables we chose to investigate. In the case of regional richness, its unique importance would have been overestimated by over 100%. In general, studies examining either the local environment or regional richness in isolation risk overemphasizing the importance of the chosen predictors due to the underlying covariance with unconsidered predictor variables. While this is a general problem in regression analyses, it is particularly relevant here because there are many reasons to think that regional richness might frequently co-vary with local environmental variables (Harrison et al. 2006; Harrison and Cornell 2008). The collinearity between regional richness and local environmental variables also has consequences for the interpretation of individual predictors on local richness (Graham 2003). For example, the coefficient for regional richness decreases by 70% when local environmental variables are added to the model (Appendix A). Such differences will be crucial when attempting to evaluate theories that make specific predictions about model parameters (e.g., Allen et al. 2002; Algar et al. 2007; Hawkins et al. 2007), because if the contribution of regional enrichment is not controlled for then the wrong estimate of the fitted parameter may be compared to the theoretical value.

In addition to yielding improvements in overall model fit and parameter estimation, the

combined model substantially decreases the spatial structure of model residuals. The raw

richness values exhibit significant spatial autocorrelation at distances up to ~1500 km (fig. 2),

which could present a problem for modeling the data using non-spatial methods (Lennon 2000).

The residuals of the regional enrichment model display similar spatial autocorrelation (fig. 2).

Modeling richness with local environmental data reduces autocorrelation in the residuals (see

also Hurlbert and White 2005; Hortal et al. 2008), although smaller scale positive autocorrelation

remains in the shortest distance class. The model combining local environmental factors and

regional richness eliminates this remaining residual autocorrelation resulting in no significant

autocorrelation at any scale (fig. 2). This suggests that the residual spatial structure in some local

scale species richness models may be due to the enrichment of local communities by the regional

species pool, potentially reducing the need for spatial regression techniques when richness is

modeled using a combined approach (Diniz-Filho et al. 2003).

While the inclusion of both regional richness and local environmental variables in a single

analysis of species richness is relatively rare (Harrison and Cornell 2008), it is more common to

see different scales of environmental variables evaluated in the same analysis (e.g., Rahbek and

Graves 2001; Hurlbert and Haskell 2003). More sophisticated analyses using structural equation

modeling will be required to tease apart the details of how regional and local environments

influence regional and local richness and the effect of regional richness on local richness. That

said our results are qualitatively similar when using different scales of environmental variables

and our simple path analysis supports our general conclusions (Appendix A).

Spatial scale, autocorrelation, and "pseudoreplication"

Analyses similar to ours have been criticized as being pseudoreplicated due to the spatially

autocorrelated nature of the regional species pool (Srivastava 1999). For example, in this study

the median percentage of shared species among all pairwise regional pool comparisons was 32%.

However, the regional species pool is no different than any other spatially autocorrelated

predictor variable. For example, at the scale at which birds perceive elevational differences most

of the Midwest is a single elevational "region". This autocorrelation results in an overestimate of

the number of degrees of freedom if autocorrelation persists in the model residuals (e.g.,

Lichstein et al. 2002). To be clear, the pseudoreplication described by Srivastava (1999) in this

observational context is simply spatial autocorrelation. Because our central analysis is that of the

combined model and the combined model successfully removes spatial autocorrelation from the

residuals, our analysis does not overestimate the degrees of freedom and thus yields valid

statistical results (Lichstein et al. 2002; Diniz-Filho et al. 2003; Rangel et al. 2006). Srivastava

(1999) recommends that in order to avoid pseudoreplication, local richness values should be

averaged to produce only a single value for each broadly defined geographic region. Our

analyses support the idea that models based solely on regional richness will exhibit strong

autocorrelation (fig. 2) and therefore support Srivastava's (1999) concern with respect to

non-combined analyses as described above. However, her proposed solution of averaging data

points within regions eliminates all within-region variability in local richness, and is thus

inappropriate for assessing the relative importance of the local environment which may be

important in driving that variability. Studies of local-regional relationships that remove local

scale variability by averaging local richness values within a larger region (e.g., Srivastava 1999,

Karlson et al. 2004) ignore this meaningful variation and may exaggerate the importance of the

regional pool. Our combined model solves this problem by successfully modeling the observed

autocorrelation as being driven by meaningful environmental variation and regional enrichment

and thus allows individual local scale data points to be incorporated without statistical

complications. More sophisticated spatially explicit modeling may well provide key additional insights, but the current approach represents a valuable first step towards understanding these patterns.

Temporal scale and the relative importance of local and regional processes

We explored the influence of the temporal resolution used to characterize local species richness and found that increasing the time-scale has only a small influence on the overall predictive power of the regression model (fig. 3). However, the proportions of the variance explained by the local environment and regional enrichment changed as the time-scale increased (fig. 3). While local environmental variables largely dominate at one-year timescales, at decadal timescales, local and regional variables explain similar amounts of variance in local richness. The processes governing species richness are expected to change with the scale of analysis due to changes in the physical and biological processes dominating at different scales (Holling 1992). For example, species interactions occur over days and hectares whereas speciation dynamics occur over regional to continental extents and geological time periods. As such, it makes sense that regional processes play an increasing role at longer time scales. These results confirm the suggestion that temporal scale should affect the strength, as well as the shape, of the local-regional richness relationship (Srivastava 1999).

The changes in explained variance result from changes in cumulative local richness with time-scale. The accumulation of species occurs due to both increased sampling intensity, whereby rare species that were present at the site are finally sampled, and real turnover, where species that were not present in a given year colonize the site (White 2004, White et al. 2006). Species in this latter group include both vagrants and species invading the site in response to changes in environmental conditions. Thus, the species richness of a local site over a broader

temporal window increasingly reflects temporal beta diversity relative to single year alpha

diversity, and it has been shown that beyond time-scales of ~2-3 years that this beta diversity is

driven more by ecological processes than sampling intensity (White 2004). As such, our results

suggest that local environmental constraints are most important for determining alpha diversity

in North American bird communities, while regional enrichment is important for explaining

patterns of temporal beta diversity. In the face of environmental variability, richer regional

species pools are more likely to contain species that can successfully cope with novel conditions.

In addition, even in the absence of environmental change, richer species pools are expected to

contribute more species to local communities via mass effects (*sensu* Shmida and Wilson 1985).

This suggests a possible avenue for integrating local and regional influences on species

richness. It has been proposed that local communities are actually composed of two potentially

discrete groups of species: 1) core (or source) species, which maintain viable populations at a site

because they are well suited to the local ecological conditions; and 2) occasional (or sink or

vagrant) species that periodically occur at the site through random colonization events, but fail to

persist in the system (MacArthur 1960; Magurran and Henderson 2003; Belmaker 2009). Since a

site will typically contain some occasional species, this would explain the unique contribution of

regional enrichment, even at the shortest time-scales. If this hypothesis is valid then observed

regional influences may occur via mass effects with the number of core species limited by local

environmental conditions and the number of occasional species influenced by the richness of the

regional pool. The ability of local environmental variables to explain one-year richness values

may thus reflect the constraints imposed by the local environment that limit the number of core

species which can maintain stable populations at that site. Vagrant species would not be expected

to be restricted by this limited capacity as only a few dispersing individuals are encountered

(MacArthur 1960; Magurran and Henderson 2003; Belmaker 2009). The fact that regional richness becomes increasingly important for understanding local richness over longer temporal windows reflects the fact that the number of species that might ephemerally colonize a site should increase with the time period of sampling (Grinnell 1922) and the size of the species pool. Thus occasional species richness should be driven by regional enrichment and should be more prevalent at longer time scales. Admittedly this clear distinction between core and occasional species is overly simplistic. For example, the status of species can change through time in response to changing environmental conditions or biotic interactions (Brown et al. 2001). In addition, distinguishing between core and occasional species will often be difficult and might require choosing an arbitrary cutoff based on abundance or persistence (e.g., Magurran and Henderson 2003).

Finally, it is also worth noting that as time scale increases there is an increase in the proportion of variation that cannot be uniquely ascribed to either local or regional influences, and thus, the relative contribution of these processes becomes less distinguishable (fig. 3). As a result analyses that use local richness measures based on longer time scales, e.g. regional floral and faunal lists, risk overestimating the importance of either local or regional processes if both are not examined simultaneously using this type of variance partitioning framework.

Online Appendix A. Supplemental Methods and Results.

Path analysis – detailed methods and results

We conducted a simple path analysis using least squares methods to explore the manner in which regional scale climate influenced local scale richness. For simplicity we: 1) only analyzed the single most important climate variable (summer NDVI; univariate correlations were equivalent for NDVI and NDVI^2 so we chose the linear form for direct comparison with Harrison et al. 2006); 2) used only the most important transformation of regional richness (the untransformed data); and 3) used all of the data instead of separating it into training and validation sets. The results (Figure S2) indicate that most of the contribution of regional scale NDVI (defined as the average NDVI within a 320 km radius circle of the starting location of the route) on local richness was through its influence on local NDVI and local NDVI's influence on richness (0.46). The influence of regional NDVI though regional richness was relatively minor (0.12). This result is contrary to that of Harrison et al. (2006; see also Harrison and Cornell 2008) who show that for serpentine plant communities in CA that regional NDVI's influence occurs primarily through its influence on regional richness.

Table S1. Parameter estimates and multivariate statistical results for the three statistical models.

MODEL AND PARAMETER	PARAMETER ESTIMATE [95% CI]	P-VALUE	MODEL R^2
Regional Enrichment			0.331
$RegRich$	1.21 [0.73, 1.69]	$<10^{-6}$	
$RegRich^2$	-0.004 [-0.007, -0.001]	0.007	
Local Environment			0.572
$SumTemp$	2.11 [-0.03, 4.24]	0.054	
$SumTemp^2$	-0.05 [-0.103, 0.005]	0.078	
$WinTemp$	-0.14 [-0.57, 0.29]	0.517	
$WinTemp^2$	-0.04 [-0.05, -0.02]	$<10^{-4}$	
$AnnPrecip$	0.003 [-0.008, 0.014]	0.568	
$AnnPrecip^2$	-4.70e-6 [-8.35e-6, -1.06e-6]	0.012	
$SumNDVI$	15.6 [-29.5, 60.8]	0.498	
$SumNDVI^2$	55.7 [13.4, 98.0]	0.010	
$WinNDVI$	42.8 [14.5, 71.2]	0.003	
$WinNDVI^2$	-60.8 [-100.1, -20.8]	0.003	
$Elev$	-0.008 [-0.015, -0.002]	0.014	
$Elev^2$	3.08e-6 [7.60e-7, 5.40e-6]	0.010	
Combined Model			0.677
$RegRich$	0.36 [-0.17, 0.90]	0.184	
$RegRich^2$	6.02e-4 [-2.57e-3, 3.78e-3]	0.710	
$SumTemp$	-0.84 [-2.96, 1.27]	0.435	
$SumTemp^2$	0.03 [-0.02, 0.09]	0.248	
$WinTemp$	-0.10 [-0.51, 0.31]	0.630	
$WinTemp^2$	-0.02 [-0.04, 0.002]	0.085	
$AnnPrecip$	-4.13e-4 [-0.01, 0.01]	0.938	
$AnnPrecip^2$	-1.70e-6 [-5.19e-6, 1.78e-6]	0.338	
$SumNDVI$	77.8 [33.1, 122.5]	0.001	
$SumNDVI^2$	-29.0 [-73.5, 15.4]	0.201	
$WinNDVI$	34.2 [6.81, 61.5]	0.015	
$WinNDVI^2$	-42.2 [-82.4, -2.00]	0.040	
$Elev$	-6.65e-3 [-1.27, -4.21e-4]	0.015	
$Elev^2$	6.58e-7 [-1.57e-6, 2.88e-6]	0.563	

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Figure Legends

Figure 1: Comparison of models of local species richness (at the five-year time scale) based on

regional richness, local environmental factors, and both combined. For illustrative purposes plots

a-e include data for all sites with predicted values and residuals based on the models generated

using the data reserved for model building. In plots b, d, and e the plus symbols indicate data

used to build the model and the circles indicate data used to test the model. (a) Observed local

richness as a function of predicted local richness based on the Regional Enrichment model, color

coded by summer NDVI, the single best environmental predictor of local richness. Results are

plotted as an interpolated surface of NDVI values (color coded as quantiles) to allow the clear

presentation of large numbers of overlapping points. The solid line is the 1:1 line. (b) Residuals

of the Regional Enrichment model as a function of summer NDVI. (c) Observed local richness as

a function of predicted local richness based on the Local Environment model, with points color

coded by regional richness (plotting details as in (a)). (d) Residuals of the Local Environment

model as a function of regional richness. (e) Observed vs. predicted plot for the Combined model

including both regional richness and local environmental factors. (f) Comparison of the

performance of the three models based on proportion of variance explained. The Combined

model's variance is partitioned to show the unique contributions of the local environment (blue),

regional richness (red), and the variance that is described by some combination of the two sets of

factors, but is not uniquely ascribable to either (grey). Only data reserved for model testing was

used for this final analysis.

Figure 2: Patterns of spatial autocorrelation (Moran's *I*) at the five year time-scale for the raw

richness data (black) and the residuals of the three models: Regional Enrichment (red), Local

Environment (blue), and the Combined model (green). Confidence intervals (error bars) for

Moran's *I* are Bonferroni corrected for the number of distance classes (i.e., error bars are equal to

$\pm\, 3.08{\times}\sigma_I$

). Zero autocorrelation is shown by the dashed black line.

Figure 3: Effect of time scale on the partitioning of variance of species richness in North

American breeding birds into effects of the local environment (blue), regional enrichment (red),

and variance explained by some combination of the two sets of factors that cannot be uniquely

ascribed to both (grey).

Figure S1. Map of routes from the Breeding Bird Survey of North America that were analyzed in

this study.

Figure S2. Results of the path analysis evaluating the manner in which regional scale climate

influences local scale richness. Most of the contribution of regional scale NDVI (defined as the

average NDVI within a 320 km radius circle of the starting location of the route) on local

richness was through its influence on local NDVI and local NDVI's influence on richness (0.46).

The influence of regional NDVI though regional richness was relatively minor (0.12). See

Online Appendix A for details.