Energy hypothesis included in this study

Energy

The energy hypothesis has been mechanistically connected to species richness in a number of different ways (Evans et al. 2005). The possibilities that have received the most recent attention are effects of temperature on metabolism, and effects of energy availability on species extinctions. When thinking about energetic determinants of species richness, it is important to differentiate among two types of energy: kinetic and potential (Allen et al. 2007). Kinetic energy refers to temperature, and it affects ectothermic organisms primarily by influencing metabolic rates. Temperature can increase mutation rates (Rohde 1992, Gillooly et al. 2005, Allen and Gillooly 2006), and decreases generation time (Gillooly et al. 2002). This has the potential to promote evolutionary rates, leading to elevated species richness in places with high temperatures. In contrast, potential (or chemical) energy refers to energy stored in biomolecules produced primarily by photosynthesis. At local scales, potential energy has been linked to species richness through its effects on population size. More food (potential energy) potentially translates into larger or denser populations. In turn, populations with large numbers of individuals are less likely to go extinct (more individuals hypothesis: Srivastava and Lawton 1998). A number of theoretical and empirical studies have documented the relationship between extinction probability and number of individuals (Lande 1993, Lynch et al. 1995) or range size (Jones et al. 2003). This could produce species-rich biotas in highly productive areas due to reduction in extinction rates. Additionally, since energy transmission across the food web is inefficient, species in high trophic levels tend to be the most energy-constrained, and less abundant; this could cause part of the reduction in species richness to be the result of loss of species at the top of the food web, and produce an association between energy availability and number of trophic levels (Kaunzinger and Morin 1998, but see Post 2002).

A final consideration related to the energy hypothesis is that water can play an important role in mediating energetic effects. Water is fundamental in transformation of light energy into potential energy by photosynthesis, and water is also fundamental in transfer of energy produced by autotrophs to higher levels of the food web. Consequently, water availability can be an important constraint on creation and transfer of potential energy and can play a fundamental role in effects that energy has on species richness (Evans et al. 2005).

These and various other explanations for the strong species-energy relationships observed have been proposed (Evans et al. 2005). But, the exact way by which energy affects taxonomic diversity is still unknown since all possibilities lack strong empirical support. For example, the strong species-energy relationship is true for both endotherm and ectotemrs, yet the effects of temperature on metabolic rates are mostly restricted to ectotherm organisms (Hawkins et al. 2007). Similarly, the more individuals hypotheses requires that places with higher species richness have also populations that are denser, and this has found not to be the case (Currie et al. 2004). Much work will be necessary to clarify the mechanisms behind the frequent richness-energy relationships.

Environmental heterogeneity

Environmental heterogeneity can occur in at least two forms: topographic complexity or habitat variability (Ruggiero and Hawkins 2008). Topographic complexity potentially increases number of barriers to dispersal (Simpson 1964), thereby reducing gene flow and increasing population subdivision. In turn, populations isolated from one another can speciate allopatrically. This process can lead to high species richness in topographically heterogeneous regions. Besides topographic complexity, habitat variability can also have an effect on species richness. High habitat variability provides a broader niche space, or “more niches” (MacArthur 1964). At local scales, this offers a scenario where a higher number of species can co-exist in a community by occupying different portions of the niche space. At a regional scale, high spatial habitat variability can produce elevated levels of species turnover across communities, leading to regions with high species richness independently of richness at local levels. Additionally, habitat variability can affect speciation rates by allowing an original species to split into two or more descendents species through parapatric speciation (Rosenweig 1995, Graham et al. 2004).

Seasonality

Seasonality can be considered a form of environmental heterogeneity that occurs along a temporal dimension, and has been both positively and negatively associated with species richness. On one hand, similar to the effect produced by spatial environmental heterogeneity, seasonality could provide the template for species to specialize and coexist by occupying different portions of the temporal niche dimension (Tilman et al. 1993). In contrast, seasonality has been proposed as a source of environmental instability (e.g. wide temperature fluctuations). This temporal environmental instability can generate wide population fluctuations, which have been shown to significantly increase extinction risk (Inchausti and Halley 2003). Additionally, species may ameliorate the problem of temporal variability by developing broad niches (Pianka 1966, MacArthur 1972). At local scales, broad niches can lead to species-poor communities due to lack of fine partitioning of niche space (MacArthur 1972). At larger scales, broad niches can lead to species with large geographic distributions, with few ecological barriers to
dispersal, and little population subdivision, which in turn would reduce the likelihood of speciation events.

References


Rosenzweig, M. L. 1995. Species diversity in space and time. – Cambridge Univ. Press.


Figure S1. Spatial distribution of environmental characteristics used to predict bat species richness estimated in each 100 by 100 km cell for which species richness data were obtained. First row: energy variables. (A) Average net primary productivity (g of Carbon yr\(^{-1}\) × 1,000,000,000); (B) average annual precipitation (mm); (C) average mean annual temperature (°C). Second row: heterogeneity variables. (D) Elevation standard deviation (masl); (E) NPP standard deviation (g of Carbon yr\(^{-1}\) × 1,000,000,000); (F) annual precipitation standard deviation (mm); (G) mean annual temperature standard deviation (°C). Third row: seasonality variables. (H) Average coefficient of variation of monthly precipitation; (I) average monthly standard deviation of temperature (°C).
Figure S2. Correlations among logarithms of predictor variables. Top matrix presents scatterplots, bottom matrix presents Pearson correlation coefficients. In scatterplots, lines represent linear regression fits. Points vary in gray intensity depending on species richness; light gray corresponds to low species richness; dark gray corresponds to high species richness.
Table S1. Detailed results of variation partitioning analyses. First column describes the different fractions of variation defined in Fig. 2. The second column defines fractions of variation in terms of environmental hypotheses. Results are presented for richness gradients of all bats, and for that of each species group based on geographic range size (see text for details). For each combination of variation component and richness gradient, adjusted R² and its confidence interval are presented. Those adjusted R² values in bold were statistically greater than expected by chance according to a permutation test (see text for details). e: energy, h: heterogeneity, s: seasonality, U: union, ∩: intersection, |: after accounting for, n: number of cells used for analysis, CI: confidence interval.

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<th>3rd group (n=3128)</th>
<th>2nd group (n=2268)</th>
<th>1st group (n=708)</th>
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<td></td>
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<td>95% CI</td>
<td>Adj. R²</td>
<td>95% CI</td>
<td>Adj. R²</td>
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<td>0.920</td>
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<td>0.850</td>
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<td>0.000 0.000</td>
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<td>0.070</td>
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</table>
R code

Code to run variation partitioning analyses, calculate bootstrapped confidence intervals, and perform permutation test

#####################################################################
#### FUNCTION: “enviro.analyses”. A function to estimate correlation of richness with environmental and spatial predictors, calculate confidence intervals by bootstrapping or subsampling, and perform a permutation test of difference from random. Variation in dependent variable (“richness”) is partitioned into fractions of variation in two hierarchical steps. First, variation is partitioned between spatial predictors (produced from argument “coords”) and all environmental predictors (combination of arguments “X1”, “X2”, and “X3”). Second, variation is partitioned among environmental predictor sets (given by arguments “X1”, “X2”, and “X3”). Variation partitioning is carried out by the function “varpart”, provided in the package “vegan”. A description of variation partitioning analysis can be found in Borcard et al. (1992) and Legendre and Legendre (1998). Proportions of variation in these analyses are estimated by adjusted R-square values following Peres-Neto et al. (2006). Additionally, single variable regressions are produced between the dependent variable and each of the variables in the environmental predictor matrices. Disclaimer: This code is provided “as is”, without warranties of any kind. Users of this function are cautioned that, while due care has been taken and the code is believed accurate, it has not been rigorously tested and its use and results are solely the responsibilities of the user.

## ARGUMENTS:

# richness: a vector length “n”, where “n” is the number of observations. These richness values are used as the dependent variable.

# coords: a matrix of dimensions “n” by 2, which contains coordinates for the spatial location of each value of richness. Columns of this matrix must be labeled “x” and “y”, and order of the columns does not matter. A set of spatial predictors are produced from these coordinates. These spatial predictors are all elements of a polynomial of degree given by the argument “space.poly.degree” (Legendre and Legendre 1998, pages: 739-745).

# X1, X2 and X3: three matrices of dimensions “n” by “p”, where “p” is number of predictors included in a given matrix. These matrices are used as sets of explanatory variables. Each matrix has to represent a different hypothesis, for example: energy, heterogeneity and seasonality.

# rand.type: a character argument indicating whether bootstrap or subsampled confidence intervals are required (options “bootstrap.CI” and “subsampling.CI” respectively) or permutation test of difference from random is required (option: “permutation.test”). For the “bootstrap.CI” option, the “richness” vector and the rows in “coords”, “X1”, “X2” and “X3” matrices are sampled with replacement to create new variables to conduct analyses in each randomization. For the “subsampling.CI” option, the original “richness” vector and predictor matrices are sampled at random to built smaller datasets for analyses in each randomization. The number of observations to be incorporated into these new dependent and independent variables is determined by the argument “subsample.n”. For this option, if “subsample.n” is equal to the number of observation in the original variables, then analyses in each randomization are the same as the analyses for the original variables. For the “permutation.test” option, the “coords”, “X1”, “X2”, and “X3” matrices are left unmodified, but the “richness” vector is randomly reordered; in this way the associations of richness with values in the explanatory variables is destroyed. This option is also modified by the argument “subsample.n” since the observations included in the permutation test are a subset of size “subsample.n” of the original data.

# rand.n: a non-negative integer value providing the number of randomizations to be performed.

# subsample.n: a positive integer value providing the number of observations that will be used for analyses during randomizations in options “subsampling.CI” and “permutation.test” of argument “rand.type”. See argument “rand.type” for detail.

# write.res: a logical argument indicating whether the results should be written into files. In case of TRUE,
results will be written into two files. One presents the summarized results, and the other contains the detailed results coming from each randomization.

# res.name: a character argument to be used as part of the name for the files to be written with the results.

# space.poly.degree: a positive non-zero integer that gives the degree of the polynomial that is built from the coordinates in argument "coords" to represent the spatial predictors in analyses.

# print.progress: a logical argument defining whether progress on randomizations should be printed on the screen.

# zero.rich.rm: a logical argument defining whether observations where the dependent variable equals zero should be excluded from analyses.

# use.anal: a vector of length “n” that defines which observations to use for analyses and which not to use. Observations to use need to be represented by 1’s, and observations to remove should be represented by 0’s.

## OUTPUT:

# the output of this function consist on a list of 4 elements.

# 1) original_n: a scalar defining what the sample size of the original data is.

# 2) randomizations_n: a scalar defining what the sample size used for randomizations is.

# 3) summary_results: a matrix with summarized results from all simulations. This includes the a) empirical or original estimates for each coefficient or fraction of variation, b) average coefficient estimates from randomizations, and c) 95% confidence intervals (if “rand.type” is set to “bootstrap.CI” or “subsampling.CI”) or critical values for alpha 0.05 and 0.025 (if “rand.type” is set to “permutation.test”).

# 4) randomization_details: a matrix containing coefficient estimates produced by each randomization.

## CITED LITERATURE:


environ.analyses<-function(richness, coords, X1, X2, X3, rand.type="bootstrap.CI", rand.n=0, subsample.n=length(richness), write.res=F, res.name="results", space.poly.degree=3, print.progress=FALSE, zero.rich.rm=TRUE, use.anal=rep(1, length(richness)))
{
  coords<-as.data.frame(coords)
  X1<-as.data.frame(X1)
  X2<-as.data.frame(X2)
  X3<-as.data.frame(X3)

  coords<-coords[use.anal==1,]
  X1<X1[use.anal==1,]
  X2<X2[use.anal==1,]
X3<-X3[use.anal==1,]
richness<-richness[use.anal==1]

if(zero.rich.rm==TRUE)
{
    coords<-coords[richness>0,]
    X1<-X1[richness>0,]
    X2<-X2[richness>0,]
    X3<-X3[richness>0,]
    richness<-richness[richness>0]
}

environment<-data.frame(X1, X2, X3)
space<-poly(as.matrix(cbind(coords$y, coords$x)), degree=space.poly.degree)

if(length(richness)!=nrow(X1) | length(richness)!=nrow(X2) | length(richness)!=nrow(X3) |
length(richness)!=nrow(coords)) stop("error: length of richness vector do not match number of rows in explanatory matrices")

library(vegan)

var.res.names<-c(names(X1), names(X2), names(X3))
var.res.names<-paste(rep(var.res.names, each=4), rep(c("_interc", "_B", "_r2", "_adjr2"), length(var.res.
names)), sep="_")
var.res.names<-as.character(var.res.names)

rand.results<-as.data.frame(matrix(NA, 22+length(var.res.names), 5))

if(rand.type=="bootstrap.CI" | rand.type=="subsampling.CI") names(rand.results)<-c("coefficient_name", "original_estimate", "mean_RandomEstimates", "low_CI", "high_CI")
if(rand.type=="permutation.test") names(rand.results)<-c("coefficient_name", "original_estimate", "mean_RandomEstimates", "low_CritVal", "high_CritVal")

rand.results[,1]<-c("rich_lat", "full_model", "space_full", "enviro_full", "space_not_enviro", "space_intersect_enviro", "enviro_not_space", "full_model_residuals", "X1_full", "X2_full", "X3_full", "X1+X2", "X1+X3", "X2+X3", "a", "b", "c", "d", "e", "f", "g", "h", var.res.names)

abs.y<-abs(coords$y)
lat.rich<-summary(lm(richness~abs.y+I(abs.y^2)))$r.squared

data.varpart.se<-varpart(richness, space, environment)
attach(data.varpart.se$part)
res.se<-c(fract$Adj.R.square[c(3,1,2)], indfract$Adj.R.square[c(1,2,3,4)])
detach(data.varpart.se$part)

data.varpart.ee<-varpart(richness, X1, X2, X3)
attach(data.varpart.ee$part)
res.ee<-c(fract$Adj.R.square[c(1:6)], indfract$Adj.R.square)
detach(data.varpart.ee$part)
sing.var.res<-numeric()
for(j1 in 1:length(names(X1)))
{
    sing.var.res<-c(sing.var.res, summary(lm(richness~X1[,j1]))$coefficients[1], summary(lm(richness~X1[,j1]))$coefficients[2], summary(lm(richness~X1[,j1]))$r.squared, summary(lm(richness~X1[,j1]))$adj.r.squared)
}
for(j2 in 1:length(names(X2)))
{
    sing.var.res<-c(sing.var.res, summary(lm(richness~X2[,j2]))$coefficients[1], summary(lm(richness~X2[,j2]))$coefficients[2], summary(lm(richness~X2[,j2]))$r.squared, summary(lm(richness~X2[,j2]))$adj.r.squared)
}
for(j3 in 1:length(names(X3)))
{
    sing.var.res<-c(sing.var.res, summary(lm(richness~X3[,j3]))$coefficients[1], summary(lm(richness~X3[,j3]))$coefficients[2], summary(lm(richness~X3[,j3]))$r.squared, summary(lm(richness~X3[,j3]))$adj.r.squared)
}
rand.results[,2]<-c(lat.rich, res.se, res.ee, sing.var.res)

if(rand.n>0)
{
    rand.details<-matrix(NA, rand.n, 22+length(var.res.names))
colnames(rand.details)<-c("rich.lat", "full_model", "space_full", "enviro_full", "space_not_enviro", "space_intersect_enviro", "enviro_not_space", "full_model_residuals", "X1_full", "X2_full", "X3_full", "X1+X2", "X1+X3", "X2+X3", "a", "b", "c", "d", "e", "f", "g", "h", var.res.names)

    id<-seq(1:length(richness))

    if(rand.n>0)
    {
        for (i in 1:rand.n)
        {
            if(print.progress==TRUE) print(i)
            res.i<-numeric()
            if(rand.type=="bootstrap.CI")
            {
                rand.id<-sample(id, replace=T)
                coords.<-coords[rand.id,]
                X1.i<-X1[rand.id,]
                X2.i<-X2[rand.id,]
                X3.i<-X3[rand.id,]
            }
        }
    }
}
if(rand.type=="subsampling.CI")
{
    rand.id<-sample(id, subsample.n, replace=F)
    coords.i<-coords[rand.id,]
    X1.i<-X1[rand.id,]
    X2.i<-X2[rand.id,]
    X3.i<-X3[rand.id,]
}

if(rand.type=="permutation.test")
{
    rand.id<-sample(id, subsample.n, replace=F)
    richness.i<-richness[rand.id]
    coords.i<-coords[rand.id,]
    X1.i<-X1[rand.id,]
    X2.i<-X2[rand.id,]
    X3.i<-X3[rand.id,]

    rand.id<-sample(1:subsample.n, replace=F)

    richness.i<-richness[rand.id]
    environment.i<-data.frame(X1.i,X2.i,X3.i)
    space.i<-poly(as.matrix(cbind(coords.i$y, coords.i$x)), degree=space.poly.

    abs.y.i<-abs(coords.i$y)
    lat.richness.i<-summary(lm(richness.i~abs.y.i+I(abs.y.i^2)))$r.squared

    data.varpart.se.i<-varpart(richness.i, space.i, environment.i)
    attach(data.varpart.se.i$part)
    res.se.i<-c(fract$Adj.R.square[c(3,1,2)], indfract$Adj.R.square[c(1,2,3,4) ]
    detach(data.varpart.se.i$part)

    data.varpart.ee.i<-varpart(richness.i, X1.i, X2.i, X3.i)
    attach(data.varpart.ee.i$part)
    res.ee.i<-c(fract$Adj.R.square[c(1:6)], indfract$Adj.R.square)
    detach(data.varpart.ee.i$part)

    sing.var.res.i<-numeric()

    for(j1 in 1:length(names(X1.i)))
    {
        sing.var.res.i<-c(sing.var.res.i, summary(lm(richness.
        i-X1.i[,j1]))$coefficients[1], summary(lm(richness.i-X1.i[,j1]))$coefficients[2], summary(lm(richness.
        i-X1.i[,j1]))$r.squared, summary(lm(richness.i-X1.i[,j1]))$adj.r.squared)
    }

    for(j2 in 1:length(names(X2.i)))
sing.var.res.i<-c(sing.var.res.i, summary(lm(richness.i~X2.i[,j2]))$coefficients[1], summary(lm(richness.i~X2.i[,j2]))$coefficients[2], summary(lm(richness.i~X2.i[,j2]))$r.squared, summary(lm(richness.i~X2.i[,j2]))$adj.r.squared)
for(j3 in 1:length(names(X3.i)))
{
  sing.var.res.i<-c(sing.var.res.i, summary(lm(richness.i~X3.i[,j3]))$coefficients[1], summary(lm(richness.i~X3.i[,j3]))$coefficients[2], summary(lm(richness.i~X3.i[,j3]))$r.squared, summary(lm(richness.i~X3.i[,j3]))$adj.r.squared)
}
rand.details[,i]<-c(lat.richness.i, res.se.i, res.ee.i, sing.var.res.i)
}
for(j3 in 1:length(names(X3.i)))
{
  rand.details[,j3]<-c(rand.details[,j3], sing.var.res.i)
}

rand.results[,3]<-apply(rand.details, 2, mean, na.rm = TRUE)
if(rand.type=="bootstrap.CI" | rand.type=="subsampling.CI") rand.results[,c(4,5)]<-t(apply(rand.details, 2, quantile, probs=c(0.025, 0.975), na.rm = TRUE))
if(rand.type=="permutation.test") rand.results[,c(4,5)]<-t(apply(rand.details, 2, quantile, probs=c(0.950, 0.975), na.rm = TRUE))
}
if(rand.n==0) {
  richness.i<-numeric()
  rand.details<-"randomizations not requested"
}
if(write.res==T) {
  file.name.1<-paste(res.name, "_summary.txt")
  file.name.2<-paste(res.name, "_details.txt")
  write.table(rand.results, file=file.name.1, row.names=F, quote=F, sep="\t")
  write.table(rand.details, file=file.name.2, row.names=F, quote=F, sep="\t")
}
output<-list(length(richness), length(richness.i), rand.results, rand.details)
names(output)<-c("original_n", "randomizations_n", "summary_results", "randomization_details")
output