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Source: *The American Naturalist*, (-Not available-), p. 000
Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)
Stable URL: <http://www.jstor.org/stable/10.1086/677261>
Accessed: 12/08/2014 14:50

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Asynchrony of Seasons: Genetic Differentiation Associated with Geographic Variation in Climatic Seasonality and Reproductive Phenology

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Submitted January 29, 2014; Accepted April 25, 2014; Electronically published August 6, 2014

Dryad data: <http://dx.doi.org/10.5061/dryad.40d6h>.

ABSTRACT: Many organisms exhibit distinct breeding seasons tracking food availability. If conspecific populations inhabit areas that experience different temporal cycles in food availability spurred by variation in precipitation regimes, then they should display asynchronous breeding seasons. Thus, such populations might exhibit a temporal barrier to gene flow, which may potentially promote genetic differentiation. We test a central prediction of this hypothesis, namely, that individuals living in areas with more asynchronous precipitation regimes should be more genetically differentiated than individuals living in areas with more similar precipitation regimes. Using mitochondrial DNA sequences, climatic data, and geographical/ecological distances between individuals of 57 New World bird species mostly from the tropics, we examined the effect of asynchronous precipitation (a proxy for asynchronous resource availability) on genetic differentiation. We found evidence for a positive and significant cross-species effect of precipitation asynchrony on genetic distance after accounting for geographical/ecological distances, suggesting that current climatic conditions may play a role in population differentiation. Spatial asynchrony in climate may thus drive evolutionary divergence in the absence of overt geographic barriers to gene flow; this mechanism contrasts with those invoked by most models of biotic diversification emphasizing physical or ecological changes to the landscape as drivers of divergence.

Keywords: birds, reproduction, breeding phenology, genetic distance, allochronic speciation, temporal asynchrony.

Introduction

A major goal in ecology and evolutionary biology is to understand the mechanisms responsible for the origin of extant species and of spatial patterns of biodiversity. Ultimately, diversification processes resulting from popula-

tion differentiation over spatial and temporal dimensions are responsible for contemporary species richness. Ample research has examined the role of spatial barriers in generating population structure and speciation (Mayr 1942; Coyne and Orr 2004). Not so extensively studied, however, are the roles of temporal barriers (i.e., allochronic differentiation) in diversification processes (Yamamoto and Sota 2009; Fagan et al. 2010; reviewed in Coyne and Orr 2004).

Organisms are expected to modify the timing of life-history stages to adjust to favorable environmental conditions (Wingfield et al. 1992; Durant et al. 2007; Hahn and MacDougall-Shackleton 2008). Because breeding is an energetically demanding process with obvious ties to lifetime fitness, reproduction should correlate with appropriate environmental conditions for offspring survival, such as an abundant supply of resources (Durant et al. 2007; Burger and Both 2011; Dunn et al. 2011). The precise fit between reproductive periods and favorable environmental conditions is achieved by individuals via cues reflecting changes in the environment (Hahn and MacDougall-Shackleton 2008), such that populations exhibit breeding seasons that track periods of high energy availability. It follows that if conspecific populations inhabit areas experiencing different temporal cycles in food availability, then they should display asynchronous breeding seasons. If stable over time, then such asynchronous reproduction between populations might limit gene flow, thereby potentially promoting genetic differentiation.

Breeding activity is often related to temporal variation in precipitation, especially in tropical organisms (van Schaik et al. 1993; Shine and Brown 2008). Because precipitation is strongly related to food availability (Ahumada 2001; Wright and Calderón 2006), tropical animals are expected to adjust their reproductive timing to match local precipitation patterns (Hau et al. 2008; Shine and Brown 2008; Martin et al. 2009; Jahn et al. 2010), which may be

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Am. Nat. 2014. Vol. 184, pp. 000–000. © 2014 by The University of Chicago. 0003-0147/2014/18403-5525\$15.00. All rights reserved.

DOI: 10.1086/677261

variable even over small spatial scales (Legates and Willmott 1990). Thus, due to spatial variation in precipitation regimes, different locations may exhibit temporal asynchrony in pulses of food supply, which may result in distinct reproductive schedules among populations reflecting either local evolutionary adaptation or phenotypic plasticity (Hahn and MacDougall-Shackleton 2008; Charmantier and Gienapp 2014). If asynchronous reproduction in relation to spatial variation in climatic seasonality (hence, resource availability) leads to divergence between populations, then increasing seasonal asynchrony should be positively correlated with population differentiation and, eventually, reproductive isolation (Martin et al. 2009). This postulate, known as the asynchrony of seasons hypothesis (ASH; Martin et al. 2009), has not been formally tested but is based on evidence suggesting that spatial variation in precipitation seasonality may lead to breeding allochrony and population differentiation. For example, two tropical populations of rufous-collared sparrows (*Zonotrichia capensis*) located only 25 km apart experience different rainfall patterns that trigger asynchronous breeding seasons, which, combined with female preference for local songs, likely drive their observed genetic and cultural differentiation (Moore et al. 2005; Danner et al. 2011; see also Jacobs and Wingfield 2000).

Birds are an appropriate model to study seasonal breeding patterns in relation to climatic variation and their association with patterns of genetic differentiation. Birds exhibit marked breeding seasonality both in temperate zones and in tropical latitudes (Dittami and Gwinner 1985; Wingfield et al. 1992; Jacobs and Wingfield 2000; Hau et al. 2008). During the breeding season, birds adjust hormonal profiles and grow their gonads to become functional (Wingfield et al. 1990); when the breeding season ends, gonads are regressed and become inactive (Wingfield et al. 1992; Gill 2007). Some tropical species exhibit a more plastic reproductive phenology, breeding opportunistically in environments with high climatic variability (Wikelski et al. 2000), whereas others seem to have an internal, fixed rhythm (Lofts 1964; Moore et al. 1983; Scheuerlein and Gwinner 2002). However, because maintaining functional gonads throughout the year is energetically costly and because birds have high energy turnover relative to body weight and are unable to store large amounts of resources, they are income breeders tightly dependent on food availability (Martin 1987). Several studies suggest that the onset of the breeding season in tropical birds is triggered by rainfall and its associated pulses in food abundance (e.g., Lofts 1964; Lofts and Murton 1968; Poulin et al. 1992; Hau et al. 2008). Thus, one expects individuals dispersing into a population with a distinct precipitation regime to experience reduced fitness owing to a mismatch in breeding condition with respect to local individuals. Although

this mismatch may be overcome via plastic adjustments in some cases (Charmantier and Gienapp 2014; Martin et al. 2014), in a given breeding season, immigrants are still expected to be at a disadvantage due to a time lag in gonadal development. If distinct breeding schedules reflect evolved differences resulting from local adaptation, then one expects the reduction of fitness in immigrants to be even stronger.

Here, we examine the hypothesis that spatial asynchrony in reproduction promotes genetic differentiation in birds across multiple species. Specifically, we use climatic and DNA sequence data to test whether differences in precipitation seasonality are associated with genetic differentiation among conspecific populations. We predict that individuals living in environments with asynchronous precipitation regimes will be more genetically differentiated than individuals living in environments with similar rainfall regimes, regardless of the geographic or ecological distance between them (fig. 1).

Methods

Bird Data and Genetic Distances

We tested the ASH using a broad-scale approach involving several bird species. We searched the literature for studies describing intraspecific genetic variation for which geographic information on the location of collecting sites was accessible. Our sampling was focused in the New World tropics, where precipitation asynchrony is most likely to influence population differentiation (Martin et al. 2009; see “Discussion”). Our initial database comprised mitochondrial DNA sequences of 1,586 individuals of 74 non-migrant New World species (table S1, deposited, along with all supplementary tables and figures, in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.40d6h> [Quintero et al. 2014]; fig. 2). For each species, sequences corresponded to either the cytochrome b (*cytb*) gene, the NADH dehydrogenase subunit 2 (*ND2*) gene, or the ATPase 8 and ATPase 6 genes (table S1); although these genes may differ in substitution rates, this does not affect our analyses of intraspecific genetic divergence, which are done species by species (see below). For each individual, the mitochondrial DNA sequence was downloaded from GenBank and the geographic coordinates were extracted from the published source. For individuals with a description of the collecting site but lacking geographic coordinates, we georeferenced the locality according to the published description; if the description was not precise enough, then we discarded the individual. Sequences were aligned using the MUSCLE algorithm in Geneious Pro 4.8.5 (Drummond et al. 2010), and we chose the best-fit model of nucleotide substitution for each set of sequences

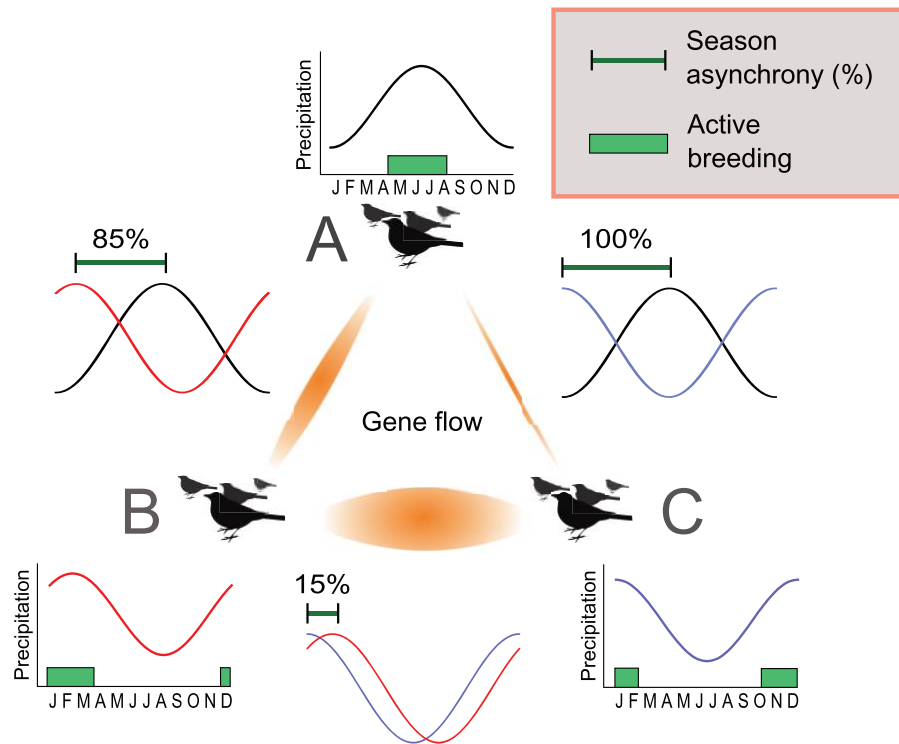


Figure 1: Spatially heterogeneous precipitation patterns may have an effect on genetic differentiation between individuals from different populations. In this hypothetical case, three conspecific populations inhabit different locations with distinct annual precipitation regimes. Within each hypothetical location, the onset of the rainy season triggers reproduction in resident birds (green bars indicate breeding seasons). The asynchrony of seasons hypothesis postulates that individuals from populations with lower asynchrony in breeding phenology (e.g., populations B and C) because they inhabit areas with similar seasonality (percentages indicate asynchrony in precipitation) will be better able to exchange genes than individuals from populations with high levels of asynchrony in breeding phenology (e.g., populations A and C) because they inhabit seasonally distinct areas.

obtained for each species using JModelTest (Posada 2008) based on the Akaike information criterion (AIC). Finally, we calculated pairwise genetic distances between all individuals of each species using the ape package, version 3.0-2 (Paradis et al. 2004) for R (R Core Team 2013). When the chosen substitution model was not available in ape, we used MEGA or PAUP* (Swofford 2003; Tamura et al. 2011). We used pairwise genetic distances between individuals instead of population-level metrics of genetic differentiation (e.g., F_{st}) because of the difficulty of defining populations given a limited number of individuals and unequal sampling across species.

Precipitation Data and Patterns of Precipitation Seasonality

Because information on local breeding schedules is lacking for our study species, we used precipitation seasonality as a proxy for food availability, which is expected to correlate with reproductive timing (Martin et al. 2009). We esti-

mated precipitation seasonality from two alternative data sources. First, we used mean monthly cloud frequency (Cloud-Cover) during the years 2000–2012 at 30-arc-second (~1 km at the equator) resolution summarized from daily MODIS MOD09GA PGE11 cloud-mask data (table S2; A. W. Wilson and W. Jetz, unpublished data). Cloud cover is strongly correlated with the mean and seasonality of precipitation (A. W. Wilson and W. Jetz, unpublished data). We also used monthly precipitation data extracted from the WorldClim database at a projected resolution of 30 arcseconds (Hijmans et al. 2005).

For each georeferenced occurrence site linked to genetic data, we extracted monthly cloud frequency data from Cloud-Cover and monthly precipitation data from WorldClim using the raster package (Hijmans 2013) for R. To describe seasonality in precipitation based on these two data sets, we employed a Fourier analysis similar to that used in a recent study on seasonality in plant phenology (Zalamea et al. 2011). This analysis computes the degree of adjustment of a time series to a periodic sinu-

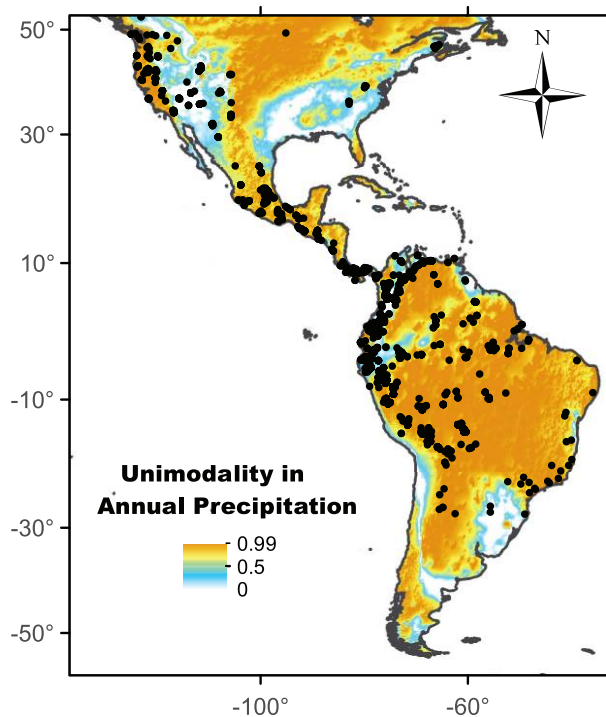


Figure 2: Map of the Americas displaying the fit of observed monthly precipitation to a unimodal sinusoidal curve as given by the Fourier analysis. Here, 1 would correspond to a perfect fit of observed monthly precipitation to an annual sinusoidal curve with one peak, and 0 would correspond to all months having the same values of precipitation. Orange indicates locations being increasingly annual in their precipitation regimes (i.e., unimodal precipitation); white indicates locations with less seasonal precipitation regimes. The locations of all individuals used in this study are indicated with black dots.

sinusoidal curve using fast discrete Fourier transformation; subsequently, the lag between any of these sinusoidal curves is estimated through a cospectral Fourier analysis. Because our time series comprises 1 year (i.e., mean monthly precipitation), a 12-month-period sinusoidal curve has only one peak and one valley, whereas a 6-month-period curve has two peaks and two valleys per year, corresponding to annual and biannual precipitation regimes, respectively. We evaluated the fit of the annual precipitation data to six different periodic components: 12, 6, 4, 3, 2.4, and 2 months. The fast Fourier transformation returns a coefficient describing the fit of the observed monthly precipitation to sinusoidal curves corresponding to each of the periodic components used (Bloomfield 2000; Zalamea et al. 2011). We created a null distribution for each locality's precipitation regime by randomly resampling 10,000 times the monthly rainfall series, from which we assessed the significance of each periodic component.

Individuals from localities with nonsignificant periodic components were discarded (182 for Cloud-Cover data and 197 for WorldClim data). All localities retained for subsequent analyses (1,404 for Cloud-Cover data and 1,389 for WorldClim data) experience either a 12- or 6-month component (i.e., annual or biannual precipitation regimes). We used a cospectral Fourier analysis to compute the lag between peaks in rainfall seasons of different localities; this analysis returns a complex vector, where the real component represents the amplitude of the frequency curve (amplitude) and an imaginary number represents the angle positioning (phase). Algorithmic subtraction between the phases of two localities results in the percentage of temporal difference between the peaks in precipitation. We used this difference as our estimate of asynchrony in precipitation seasons between localities. A 100% difference means that when one locality is in its precipitation peak, the other locality is in the lowest point of the precipitation valley (i.e., total asynchrony), and 0% indicates coincidence in precipitation peaks (i.e., no asynchrony). This analysis was performed using the `fft` function in R.

Accounting for Geographic Distance and Dispersal Barriers

Because geographic distance and geographic barriers to dispersal are major causes of population differentiation, we performed the following analyses to account for the effect of these variables on genetic divergence prior to relating genetic divergence to asynchrony in precipitation. We used species distribution modeling to create ecological resistance matrices to estimate species-specific paths of least resistance between georeferenced localities (i.e., the most probable dispersal pathways as determined by niche requirements). Subsequently, these dispersal distances were accounted for when assessing the relationship between precipitation asynchrony and genetic difference, as explained below.

First, we created a niche model for each species using the maximum-entropy algorithm MaxEnt implemented in the `dismo` package (Hijmans et al. 2013) for R. Localities for each species were obtained from the Global Biodiversity Information Facility (<http://www.gbif.org>) and published literature and were carefully vetted prior to inclusion. We excluded localities outside known distribution ranges, deleted duplicate records, and cross-referenced locality descriptions with their geographical coordinates. We did not include geographic coordinates of our georeferenced genetic data to avoid potential pseudoreplication in subsequent analyses. To create each niche model, we used current climatic data (19 variables derived from measurements of temperature and precipitation) from WorldClim and elevation data from the GTOPO30 database (Gesch et al. 1999) at a $\sim 1 \text{ km}^2$ resolution. We used a projected resolution of 0.0089°

(~1 km at the equator) encompassing most of the Americas (lat. 56°S–56°N, long. 136°W–35°W) using the raster package for R (Hijmans 2013). Additionally, we incorporated categorical land-cover data for the year 2000 from the Global Land Cover database (Bartholomé and Belward 2005). We reduced the 20 continuous variables using a principal component analysis (PCA) with prior standardization of the variables (i.e., to make each variable equally important; Crawley 2007) and then used the first five principal components (jointly accounting for >90% of the variance) and the Global Land Cover data as input variables to create the niche model for each species. Owing to the lack of real absence data, we used pseudoabsences randomly drawn from background data. We calculated the area under receiver operator curves (AUC) and model-calibrated AUC (cAUC) using cross-validation to examine the fit of each species niche model to our localities linked with genetic data (Hijmans 2013).

To estimate the likelihood of dispersal between localities linked with genetic data, we considered three different dispersal models: linear paths, least-cost paths, and randomized shortest paths (McRae and Beier 2007; Saerens et al. 2009). First, we calculated linear geographic distance, taking into account Earth's curvature. Second, we used a least-cost-path model, where the dispersal distance takes into account landscape resistance between habitat patches (Adriaenssens et al. 2003). Because the least-cost-path model assumes directionality in dispersal, which is often unrealistic, we also used randomized shortest paths, which average the distance over several Brownian-motion pathways connecting two points while accounting for environmental suitability (McRae and Beier 2007). The above analyses require a template layer from which to calculate a layer of resistance values between adjacent grid points; we used the inverse of the MaxEnt relative suitability output values, which range from 0 to 1, as resistance values. These analyses were done with the package *gdistance* (van Etten 2012) for R using parallel processors in a 48-node server. Finally, we assessed the relationship between genetic distance and each of the three dispersal models. We incorporated the best-fit dispersal model for each species as a covariate in analyses testing for the effect of differences in precipitation seasonality on genetic differentiation (see below).

Testing the Relationship between Differences in Precipitation Seasonality and Genetic Differentiation

We assessed the relationship between differences in precipitation seasonality and genetic distance separately for each species using partial Mantel tests, which use dissimilarity matrices to assess the correlation between two variables while accounting for another variable. We tested the

partial correlation between precipitation asynchrony and the genetic dissimilarity matrices conditioned on the best-fit dispersal model distance using Spearman correlation in the *ecodist* package, version 1.2.7 (Goslee and Urban 2007), for R. The significance of partial correlation was established through 10,000 permutations of one of the independent-variable matrices, and confidence intervals were estimated through bootstrapping with 10,000 iterations. Because partial Mantel tests may be biased when variables exhibit spatial autocorrelation (Guillot and Rousset 2013), we tested for spatial autocorrelation on the residuals between the best-fit dispersal model distances with genetic distance and precipitation matrices of each species using a partial Mantel correlogram (Oden and Sokal 1986).

Finally, to estimate the overall (i.e., cross-species) effect of precipitation asynchrony on genetic distances, we used a random-effects meta-analysis, which is tailored for correlation coefficients derived from multiple studies (i.e., species in our case) as input values. To consider the possible influence of nonindependence of species resulting from evolutionary relationships in our meta-analysis (Adams 2008), we tested for phylogenetic signal of the Mantel coefficient on a comprehensive supertree of birds (Jetz et al. 2012). We optimized Pagel's lambda (λ) and fitted Brownian motion, Ornstein-Uhlenbeck, and white noise (no phylogenetic signal) models of trait evolution on 1,000 randomly sampled trees from the posterior distribution (see Jetz et al. 2012). We selected the best-fit model using the AIC. Because the Mantel coefficient lacked phylogenetic signal on all 1,000 trees, conducting phylogenetic meta-analysis was not necessary (table S5; Revell 2010). Finally, because some of the species in our data set were represented by a relatively small number of individuals, we examined the sensitivity of results to sample size by repeating meta-analyses excluding species with less than 5, 10, and 15 individuals.

Strength of the Asynchrony of Seasons Effect in Relation to Species Distributions and Traits

We examined several ad hoc hypotheses to try to explain the variance among species in the strength of the relationship between precipitation asynchrony and genetic difference (i.e., the correlation coefficient obtained from the partial Mantel test) while accounting for shared ancestry. The variables we examined are as follows.

Latitude. The contrasting temporal dynamics between temperate and tropical environments is expected to result in a latitudinal difference in the impact of the ASH (Martin et al. 2009). Species living in temperate latitudes experience a highly seasonal climate where temporal patterns in temperature and photoperiod are tightly correlated with food availability. Because cues are similar over wide latitudinal

belts at high latitudes (Martin et al. 2009), reproductive activity of conspecific populations tends to occur in close synchrony over large areas. The tropics are also seasonal environments, with dry and rainy seasons (Malhi and Wright 2004) and periodic changes in food availability and biotic interactions (Jacobs and Wingfield 2000; Wikelski et al. 2000; Zalamea et al. 2011). However, precipitation seasonality may change drastically even at small distances (Legates and Willmott 1990), over which tropical species are expected to display spatially asynchronous breeding (Hau et al. 2008; Shine and Brown 2008; Jahn et al. 2010). Thus, because one may predict the strength of the effect of precipitation seasonality to be stronger at lower latitudes (Martin et al. 2009), we examined the influence of the latitudinal midpoint of each species estimated according to our sampling points.

Degree of asynchrony. We considered the effect of the degree of asynchrony in precipitation because for species in which localities show greater asynchrony in precipitation, one would expect the effect of precipitation asynchrony on genetic isolation to be stronger. Thus, for each species, we considered the mean, median, maximum, and standard deviation of precipitation asynchrony between localities.

Spatial scale. Because spatial scale likely affects the opportunities for population genetic differentiation (Kisel and Barraclough 2010), we examined the effect of mean, median, maximum, and standard deviation of geographic distances between localities.

Habitat specificity. Because the range of habitats species occupy may affect diversification processes (Pianka 1969), we examined the effect of the number of different habitats occupied per species.

Body mass. Because body size correlates with dispersal abilities and thus influences genetic differentiation (Kisel and Barraclough 2010), we tested the effect of species' average body mass.

Forest strata. Birds from different vegetation strata likely differ in dispersal propensity, and this can affect genetic differentiation (Burney and Brumfield 2009). We examined this potential effect based on a discrete quantitative scale of the most frequent forest strata used by each species (1 = terrestrial, 2 = terrestrial-understory, 3 = understory, 4 = understory-midstory, 5 = midstory, 6 = midstory-canopy, 7 = canopy).

Elevation. Because precipitation regimes vary with elevation, we considered each species' mean elevation and elevational range.

The above species variables were obtained mostly from a comprehensive database (Stoltz et al. 1996) and other sources (table S6). We fitted a phylogenetic generalized least squares regression model with simultaneous maximum-likelihood optimization of the correlation structure

according to Pagel's λ (PGLS $_{\lambda}$; Hansen 1997; Revell 2010), with each of the above factors as the explanatory variables and the Mantel correlation coefficient as the dependent variable. To account for phylogenetic uncertainty, we repeated the PGLS $_{\lambda}$ using each of the 1,000 trees mentioned above. All PGLS $_{\lambda}$ analyses were performed with the *caper* (Orme et al. 2013) and *ape* (Paradis et al. 2004) packages for R. Because all of the PGLS $_{\lambda}$ analyses estimated a λ of zero, we report results based on a weighted least squares nonphylogenetic analysis, which allowed us to take into account uneven sample sizes among species.

Finally, we modeled the effect of different combinations of the above hypotheses simultaneously using weighted least squares regression. We first standardized all variables to make their effects comparable. Then, we used stepwise model selection based on the AIC and the Bayesian information criterion (BIC) to choose the most appropriate predictors of the Mantel regression coefficient. All analyses were performed in R.

Results

Overall, MaxEnt niche models showed high predictive power according to cross-validation tests with independent data, with AUC values greater than 0.9 for 41 species (55% of the total) and greater than 0.75 for 30 species (40%). Because models for three species behaved poorly (i.e., AUC scores <0.7), they were excluded from further analyses. Among the remaining species, pairwise genetic distances between individuals were best explained by linear paths in 23 species, least-cost paths in five species, and randomized shortest paths in 27 species.

In separate analyses per species, we found mixed support for our prediction that precipitation asynchrony should relate positively to genetic differentiation. Of our starting 74 bird species, 17 were discarded because of small sample sizes or poor distribution-model performance using Cloud-Cover data (11 were discarded using WorldClim data). Using Cloud-Cover to measure precipitation asynchrony, significantly positive relationships (as indicated by Mantel correlation coefficients) between precipitation asynchrony and genetic dissimilarity matrices were found in 18 (~26%) of the species studied; 19 species (~33%) showed positive but nonsignificant relationships, and 20 species (~35%) showed negative relationships, which were significant in 5 cases (~9%; fig. S1; table S3). Using WorldClim data to measure precipitation asynchrony, 17 (~27%) of the species showed significant positive relationships, 19 (~30%) showed positive but nonsignificant relationships, 20 (~32%) showed negative nonsignificant relationships, and 7 (~11%) showed significant negative relationships (fig. S2; table S3).

The meta-analysis showed a positive and significant

cross-species correlation coefficient between precipitation asynchrony and genetic differentiation using both Cloud-Cover data (combined effect = 0.21, 95% confidence interval [CI] = 0.07–0.35, $P < .001$; fig. 3) and WorldClim data (combined effect = 0.16, 95% CI = 0.04–0.28, $P = .009$; fig. S2). Three species showed significant residual spatial structure according to partial Mantel correlograms (table S4), which may result in high type I error rates (Guillot and Rousset 2013). However, these species do not seem to be biasing our overall results because they display three different relationships between precipitation seasonality and genetic distance (i.e., significantly negative, non-significant positive, and significantly positive). We obtained similar results in meta-analyses excluding species with less than 5, 10, or 15 individuals (figs. S3, S4).

We did not find any relation between the strength of the effect of precipitation asynchrony on genetic distance and the midpoint latitude of each species using either Cloud-Cover or WorldClim data. Based on Cloud-Cover data, Mantel regression coefficients were (1) weakly and positively related with forest strata ($R^2 = 0.146$, $P = .003$), maximum and standard deviation of precipitation asynchrony ($R^2 = 0.110$, $P = .012$; $R^2 = 0.135$, $P = .005$; respectively), and mean and standard deviation of geographic distances ($R^2 = 0.088$, $P = .025$; $R^2 = 0.106$, $P = .013$; respectively); and (2) negatively related with habitat specificity ($R^2 = 0.100$, $P = .016$). Full results, including those based on WorldClim data, are available in table S7.

Finally, based on Cloud-Cover data, the model favored by stepwise variable selection under the BIC included the following significant effects on the Mantel test coefficients: positive effects of body mass, standard deviation of precipitation asynchrony, and mean geographic distance, and negative effects of median, standard deviation, and maximum geographic distance ($R^2 = 0.50$ with $P < .001$; table S8). Results for stepwise variable selection using AIC were similar (table S8). Complete results based on WorldClim data are given in table S8.

Discussion

For several species of birds, our analyses support our prediction deriving from the ASH: differences in the pattern of precipitation seasonality between localities were positively associated with intraspecific genetic distances after accounting for dispersal distance. This is a novel result, indicating that spatial variation in climatic seasonality can potentially drive population differentiation (and perhaps the origin of new species) in the absence of overt geographic barriers to gene flow and requiring no physical or ecological changes to the landscape, as emphasized in most models of biotic diversification. Although previous re-

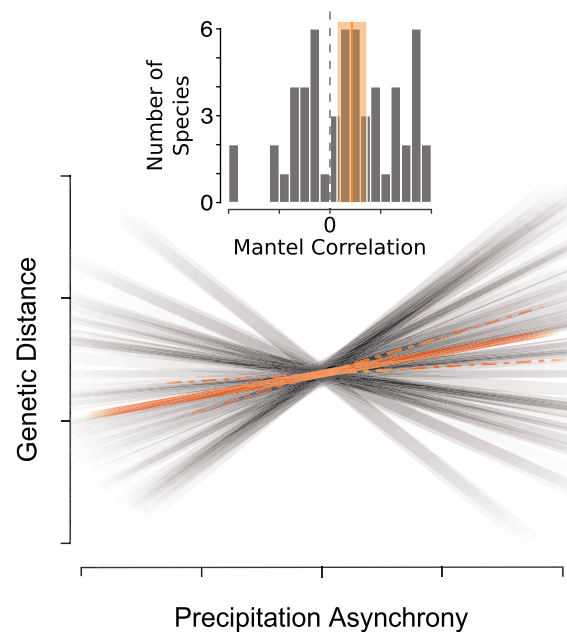


Figure 3: Overall positive effect of precipitation asynchrony (measured from Cloud-Cover data) on genetic differentiation of 57 species of birds, as given by the random-effects meta-analysis. The slopes of the gray lines in the larger pane show the correlation coefficients (ranging from -1 to 1) derived from partial Mantel tests conducted on each species. The width of lines is proportional to the standard deviation of each coefficient, and the tone of gray represents the sampling effort for each species (i.e., species with larger sample sizes are depicted with darker lines). The cross-species effect of precipitation asynchrony on genetic distance (continuous line) and its 95% confidence interval (CI; dotted lines) are shown in orange. The smaller pane shows the distribution of coefficients derived from partial Mantel tests, with the cross-species effect and its 95% CI in orange. For specific details on species-by-species tests, see table S3 and figure S1, available online.

search found evidence for a role of breeding seasonality influencing population differentiation (Hendry and Day 2005; Yamamoto and Sota 2009), a potential mechanism by which gene flow may be reduced via local differentiation of reproductive phenology in response to climatically heterogeneous environments had not been previously suggested using analyses involving a considerable number of species over a wide geographical extent.

One of the best predictors of patterns of population genetic differentiation in many of the Neotropical birds considered in our study is landscape topography (reviewed by Weir 2009, see also Gutiérrez-Pinto et al. 2012; Valdeerrama et al. 2014). Topographic features of the landscape play a fundamental role on population differentiation by limiting gene flow (e.g., across the Andes; Burney and Brumfield 2009). Because such landscape features often exhibit environmental conditions different from those fa-

vored by the study species (e.g., high temperature in low-lying valleys bisecting mountains in species restricted to cool highland areas), we accounted for their effect as physical/ecological barriers driving population differentiation, with our consideration of resistance distances derived from ecological niche models. That is, our estimates of the effect of precipitation asynchrony focus on explaining residual genetic differentiation unaccounted for by resistance distances, in principle separating the effect of topography from that of precipitation asynchrony on genetic divergence. However, one must bear in mind that topography also has an influence on precipitation (Changnon et al. 1991; Basist et al. 1994; Barnes et al. 2012). For example, spatial changes from unimodal to bimodal precipitation regimes are often associated with mountain ranges (fig. 2). This pattern, together with our results showing a positive association between precipitation asynchrony and genetic divergence, suggests that an additional effect of landscape features as drivers of population differentiation (on top of their well-appreciated role imposing physical limits to dispersal) is their influence on precipitation regimes and, hence, presumably, on timing of breeding. Nonetheless, the relationship between topography and precipitation asynchrony is not straightforward; areas with similar values of spatial asynchrony in precipitation occur in both topographically complex (mountains) and topographically uniform (lowland) regions (see fig. 2c in Martin et al. 2009). Additionally, topography is not the only factor influencing spatial changes in precipitation regimes (Bush 2005). For example, climatic cycles such as those related to movements of the Intertropical Convergence Zone lead to spatial variation in climatic seasonality, which is unrelated to topographic barriers (Krishnamurti et al. 2013). Thus, our results suggest that population divergence may arise even in the absence of topographic heterogeneity in association with spatial variation in precipitation regimes.

Whether climatic asynchrony could have driven asynchronous breeding phenologies and, eventually, genetic differentiation of populations would depend on whether the spatial pattern of climatic variation has been stable over a sufficient period of time. Our results are based only on climatic information averaged over the years 2000–2012 for Cloud-Cover data and 1950–2000 for WorldClim data, but spatial asynchrony in rainfall (and temperature) in the tropics has likely existed for millions of years (Bralower et al. 1995; Peterson et al. 2000; Chiang and Bitz 2005; Martin et al. 2009), a time span sufficient to allow for population differentiation.

Although the meta-analysis revealed an overall cross-species positive effect of precipitation asynchrony on genetic differentiation, the relationship was weak or even negative in several species. When modeled individually, the variables considered here did not explain much of the

variation across species in the strength of the effect of the ASH, suggesting that other factors need to be considered (e.g., species-specific time span of breeding, mating behavior). Unfortunately, these data are not available and gathering them would require major effort. However, the models chosen by stepwise variable selection were able to explain up to ~50% of the variance among species. Specifically, the effect of precipitation asynchrony on genetic differentiation was stronger in species with greater variation (i.e., standard deviation) in precipitation asynchrony among localities, which is expected under the ASH. In contrast to our expectations, species with greater body mass (presumably an indication of greater dispersal abilities) showed a stronger effect; a possible explanation for this pattern is that gene flow in species with greater dispersal rates may be affected to a greater extent by asynchrony in precipitation (hence, asynchrony in breeding phenology) than by physical barriers. Finally, we note that our results depended on the source of climatic data: the cross-species effect was stronger using Cloud-Cover data than WorldClim data. Because WorldClim depends on interpolation between weather stations (Hijmans et al. 2005), it is likely to miss fine-scale spatial variation and may be prone to error, especially in complex areas with few stations. Remotely sensed data do not have these limitations; thus, we consider Cloud-Cover a more robust source of data for our analyses.

Because broad-scale, cross-species data on geographic variation in breeding seasonality in relation to climatic heterogeneity are not available, especially for tropical species, a caveat of our study is that it is based on the premise that there is a precise coordination between precipitation and the activation of breeding phenology in birds. This assumption rests on evidence that precipitation regimes correlate with other climatic/environmental variables and are tightly related to food availability. Therefore, because organisms seek to reproduce during peaks of high resource availability (Wingfield et al. 1992; Durant et al. 2007; Dunn et al. 2011), even if precipitation is not the main cue used by birds to activate their phenology, other cues used to predict environmental fluctuations in food abundance are likely coupled with precipitation regimes. We acknowledge, however, that although substantial evidence supports the match between reproductive phenology and food abundance (Dittami and Gwinner 1985; Gwinner 2003), food may not be the ultimate force triggering reproduction; in some cases, predation rates or intraspecific competition might play a more prominent role (Wingfield et al. 1992; Ahumada 2001; Friesen et al. 2007).

Birds show different reproductive strategies along a continuum from circannual endogenous rhythmicity (i.e., highly heritable breeding strategies) to opportunism (Gwinner and Dittami 1990; Gwinner 2003). Species in

which timing of breeding is highly heritable are expected to have limited phenological plasticity, implying that asynchronously breeding populations would experience highly reduced effective gene flow even if they were connected by dispersal (Hendry and Day 2005; Helm 2009). In contrast, when activation of breeding phenology is entirely plastic, populations in phenological asynchrony would have lower limitations to gene flow. Existing data are insufficient to determine whether differences in breeding timing between conspecific populations of birds generally reflects adaptive and genetic-based specialization or phenotypic plasticity (Nussey et al. 2005; Charmantier and Gienapp 2014), although evidence exists for locally adapted cue-integration systems (Hahn and MacDougall-Shackleton 2008) and for high heritability in circannual rhythms (Hendry and Day 2005; Nussey et al. 2005; Versteegh et al. 2012). For instance, experiments involving translocation of individuals and monitoring of their breeding behavior have shown reduced fitness when individuals from populations breeding in asynchrony are grouped in the same place (Helm 2009; but see Martin et al. 2014).

Differences between species in the extent to which plasticity versus genetically determined reproductive timing underlie the correlation between breeding seasons and climatic seasonality might explain why some species and not others follow our prediction of greater genetic divergence between individuals living in more asynchronous localities. However, we expect that differences in phenological timing should still act as important barriers, even for species with plastic breeding schedules; because gonad activation generally takes time (e.g., 4–6 weeks; Wikelski et al. 2000; Hau et al. 2008), immigrants may be unable to match the breeding condition of local individuals. Furthermore, a phenological lag likely interacts with other factors reducing the fitness of immigrants (Burger and Both 2011). Therefore, we suggest that the ASH may partly account for patterns of population differentiation even for plastic taxa.

Allochronic speciation occurs when differences in the timing of breeding seasons act as an isolating mechanism. Because this need not require geographical isolation, allochronic speciation is often considered a special case of sympatric speciation (Alexander and Bigelow 1960; Yamamoto and Sota 2009). Evidence for allochronic speciation exists for organisms such as insects, fish, and plants (Alexander and Bigelow 1960; Simon et al. 2000; Ritchie 2001; Devaux and Lande 2008; Yamamoto and Sota 2009). For birds and other tetrapods, we are aware of only one example of allochronic speciation, which involves sympatric seabirds (Friesen et al. 2007). Importantly, the ASH does not propose that asynchrony in breeding phenology is the first step toward sympatric allochronic speciation; instead, more generally, such asynchrony is a factor preventing populations connected by dispersal from effec-

tively exchanging genes if they occur under different precipitation regimes, even if they occur in allopatry.

The ASH was first proposed by Martin et al. (2009), largely as a potential explanatory factor for the latitudinal biodiversity gradient. Because precipitation is more spatially asynchronous in the tropics than at higher latitudes, it was predicted that breeding phenologies should overlap less in the tropics, which would in turn lead to stronger population genetic structure and greater rates of speciation in tropical areas (Martin et al. 2009). However, we did not find support for the prediction that low-latitude species should be more strongly influenced by spatially asynchronous precipitation driving differences in timing of breeding and, thereby, genetic distances. We speculate that our observed lack of support for the above prediction might be the result of overall longer reproductive seasons in tropical species relative to species from the temperate zone (Ricklefs and Bloom 1977). Longer breeding seasons lead to greater potential overlap between populations in partial asynchrony, reducing the strength of precipitation-induced temporal isolation. However, our study was not specifically designed to test for an influence of latitude because most of our sampling focused on tropical species. More detailed tests of the prediction of greater influence of precipitation asynchrony on genetic divergence at lower latitudes, together with analyses of the consequences of any such pattern for the understanding of latitudinal gradients in species richness, are important priorities for future studies.

In sum, our first approach to addressing the validity of the ASH partly supports some of its components, which underscores the need to test it in greater detail. Based on our results, spatial asynchrony in climate should be considered a potential enhancer of population differentiation that may contribute to high speciation rates in climatically heterogeneous landscapes. Population differentiation within areas lacking obvious geographic barriers to gene flow is often difficult to explain; we suggest that spatial heterogeneity in precipitation regimes (ultimately, an indication of food availability) might be an important factor to consider in some species. This potential mechanism of population differentiation does not apply only to birds but also, in principle, to any other taxon exhibiting breeding seasonality coupled to seasonality in climate, including plants (Nelson 2002), invertebrates (Yamamoto and Sota 2012), and other vertebrates (Shine and Brown 2008).

Acknowledgments

We are indebted to the authors of the studies from which we obtained the data used herein, especially W. Jetz and A. W. Wilson, who shared Cloud-Cover data. We thank members of the Laboratorio de Biología Evolutiva de Ver-

tebrados at Universidad de los Andes for helpful discussions on this research. We are grateful to associate editor C. Baer as well as to W. Jetz, P. Keil, and two anonymous reviewers for comments on the manuscript. I.Q. gives special thanks to D. Plainview for inspiring dialogues.

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Associate Editor: Charles F. Baer
Editor: Troy Day



A green honeycreeper (*Chlorophanes spiza*) in Gamboa, Panama. Photo credit: F. Cediél.