Supporting Information for:
Climate change and habitat conversion favor the same species

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Supplemental Methods

Occupancy models
i) Multi-season, dynamic model to assess how a species' climate niche shapes its response to land-use

We developed a hierarchical multi-season multi-species model to estimate how a species' climate niche center and breadth along temperature and precipitation axes affect its occupancy dynamics across the land-use gradient. We evaluated only niche characteristics for mean annual temperature (Bio1) and mean annual precipitation (Bio12) from the WorldClim dataset because the niche centers of other temperature-related properties (*e.g.* temperature of warmest/coldest quarter) were all strongly correlated with Bio1 niche center (r = 0.9, 0.8 respectively) and other precipitation niche centers (*e.g.* precipitation of wettest/driest quarter) were highly correlated with Bio12 niche center (r = 1.0 and 0.8 respectively).

In the model we let $X_{i,j,t,k}$ indicate whether we detected ($X_{i,j,t,k} = 1$) or did not detect ($X_{i,j,t,k} = 0$) the i^{th} species at the j^{th} site during the k^{th} visit to that site in year t. We then let $Z_{i,j,t}$ denote the true occupancy state of species i at site j in year t ($Z_{i,j,t} = 1$ if species i was present in site j during year t and 0 if it was not). We assumed that the occupancy of species i at site j in year t was a Bernoulli random variable, such that $Z_{i,j,t} \sim \text{Bern}(\psi_{i,j,t})$ with $\psi_{i,j,t}$ denoting the probability that species i was present at site j in year t. We allowed occupancy to be the net outcome of a species' ability to persist in an already occupied site and its ability to colonize vacant sites. Thus, for the dynamic occupancy model, we investigated the effects of our variables of interest on the rates of persistence and colonization, rather than on the probability of occupancy directly.

We let $\varphi_{i,j,t}$ denote the probability that species i persisted at site j from years t to $t + 1$ (given that it was present at site j in year t) and, similarly, we let $\gamma_{i,j,t}$ denote the probability that species i colonized site j in year $t + 1$ (given that it was not present at site j in year t). The probability of occupancy for species i at site j for each subsequent year was then given by

$$logit(\psi_{i,j,t+1}) = \varphi_{i,j,t} * Z_{i,j,t} + \gamma_{i,j,t} * (1 - Z_{i,j,t}).$$

In order to quantify the effects of each land use, we defined species-specific persistence and colonization models that include the necessary covariates. Namely, we assumed that between-year persistence was given by

$$\varphi_{i,j} = \varphi 0_{i,landuse[j]} + \varphi 1_{i,region[j]} + \varphi 2_{landuse[j]} * TC[i] + \varphi 3_{landuse[j]} * TB[i] \\ + \varphi 4_{landuse[j]} * PC[i] + \varphi 5_{landuse[j]} * PB[i] + \varphi 6_{j},$$

where $\varphi0_{i,\ landuse[j]}$ denotes a species-specific intercept for each land-use category—interpreted as the mean persistence in each of the three land-uses in region 1. $\varphi1_{\mathrm{region}[j]}$ denotes a species-specific effect of region to allow each species to vary in persistence probability between regions. To avoid over-parameterizing the model, we set $\varphi1_{i,1}$equal to 0 for all species. Therefore, this parameter is interpreted as a region contrast (*i.e.,* how different is region 2, 3, or 4 from region 1). $\varphi2_{\mathrm{landuse}[j]}$ through $\varphi5_{\mathrm{landuse}[j]}$ denote the interaction effect between a species-level covariate and land-use intensity (*TC*: temperature niche center (mean of Bio1), *TB*: temperature niche breadth (SD of Bio1), *PC*: precipitation niche center (mean of Bio12), *PB*: precipitation niche breadth (SD of Bio12)). This allowed species' trait values to affect their rates of persistence differently in each land-use type. Finally $\varphi6_j$ was a random intercept for sites, included to account for consistent differences in site level persistence probability across species and years beyond that which is accounted for by land-use type. Similarly, the probability of colonization was given by

$$\begin{aligned}\gamma_{i,j} = {} & \gamma0_{i,landuse[j]} + \gamma1_{i,region[j]} + \gamma2_{landuse[j]} * TC[i] + \gamma3_{landuse[j]} * TB[i] \\ & + \gamma4_{landuse[j]} * PC[i] + \gamma5_{landuse[j]} * PB[i] + \gamma6_j,\end{aligned}$$

where the γ terms are analogous to those for persistence.

Whenever parameters were indexed by species, species identity was treated as a random effect. For example, colonization probability in transect *j* for species *i* resulted from:

$$\varphi0_{i,landuse[j]} \sim Norm(\mu.\varphi0_{landuse[j]}, \sigma^2.\varphi0_{landuse[j]})$$

Thus, for each of our three land-uses, species-specific intercepts were drawn from a normal distribution whose mean and standard deviation were estimated independently from the other two land-uses. The species-specific effect of region was parameterized equivalently (with the exception of $\varphi1_i$ and $\gamma1_i$ which were set to 0 in region one for all *i* and not estimated from the data). Note that no coefficients were indexed by year—in other words, we assumed that underlying probabilities of persistence and colonization did not change between years. Relaxing this assumption increased the number of estimated parameters in the model substantially.

Dynamic occupancy models explicitly incorporate the probability of transitioning between presence and absence across years. We therefore must initialize the first year of the model with expected occupancy probabilities. To do so, we assumed that the occupancy of species *i* in site *j* in year 1 was given by that species' equilibrium occupancy probability, based on the persistence and colonization probabilities for that site:

$$\psi_{i,j,1} = \frac{\gamma_{i,j}}{(1 - \varphi_{i,j} + \gamma_{i,j})}$$

Because not all species are present in all regions, and because we were primarily interested in how climate niche predicts relative occupancy probabilities between habitats contingent on a species existing in a region, we set all occupancy probabilities for all species never observed in a given region to zero, ensuring that those species would not influence parameter estimation in regions they were not observed.

Similar to the true occupancy state ($Z_{i,j,t}$), we assumed detection was a Bernoulli random variable such that $X_{i,j,t,k} \sim \text{Bern}(p_{i,j,t,k} * Z_{i,j,t})$, where $p_{i,j,t,k}$ was the probability that species i was detected at site j in the k^{th} sample period of the t^{th} year, given that it was present (*i.e.,* $Z_{i,j,t} = 1$). When species i was absent, $Z_{i,j,t} = 0$, and thus detection probability was 0. We allowed detection probabilities to vary by species such that the detection probability of species i at site j in the k^{th} replicate of the t^{th} year was given by

$$logit\left(p_{i,j,t,k}\right) = p0_{landuse[j]} + p1_i + p2_j + p3_t + p4_{i,j,t},$$

where the parameter set $p0_{landuse}$ describes the mean detection probability in each of the three land-uses (fixed effect), independent of species identity. Parameters p1 through p4 are random effects included to account for additional variation due to correlations between detection probabilities that are attributable to species', sites, and years. In all cases they were drawn from a normal distribution with mean 0, and standard deviation $\sigma.p1$ through $\sigma.p4$.

We analyzed the model in a Bayesian framework using vague priors throughout. We ran a total 4 chains of 15,000 iterations each, discarding the first 3,000 as burnin, with a thinning rate of 30, which yielded 1,600 posterior samples. Convergence was assessed by checking that R-hats were less than 1.1, and by visually examining the traces of the chains. We assessed model adequacy by using a posterior predictive check and calculating a Bayesian p-value (Gelman & Hill 2007). To do so, we used chi-squared discrepancy statistics. We calculated the discrepancy between the model predictions and the observed data as well as the discrepancy between the model predictions and data simulated using those predictions. At each iteration of the MCMC chain, we then calculate the Bayesian p-value as the proportion of iterations for which the discrepancy from the observed data is less than the discrepancy from the simulated data.

Goodness of fit cannot be evaluated directly for binary responses. We, therefore, followed (Carrillo-Rubio *et al.* 2014) and evaluated discrepancy by summing detections across visits, and comparing the number of visits for which each species in each site in each year was detected (0 to 3), against the expected number of detections based on fitted model parameters.

ii) Multispecies occupancy model to assess how species change habitat affiliation along a rainfall gradient

In contrast to the dynamic model in which we explicitly modeled persistence and colonization and allowed overall site occupancy to emerge as the outcome of these dynamic processes, we used a simpler model to quantify species' tendencies to shift habitat affiliations across regions. We limited our analysis to the 54 species observed in all four regions during the wet season (or 48 species observed in the dry season), because species observed in fewer regions would lend little power to conclusions regarding how habitat affiliation shifts between regions. Here occupancy probability $\psi_{i,j,t}$ is estimated according to:

$$logit(\psi_{i,j,t}) = \psi 0_{i,landuse[j]} + \psi 1_{i,landuse[j]} * RF[region[site]] + \psi 2_{i,j}$$

where $\psi 0_{i,landuse[j]}$ is a species- and land-use specific intercept, and $\psi 1_{i,landuse[j]}$ is a species- and land-use specific slope, and RF is the regional rainfall of a site. For each species i

$$\psi 0_{i,landuse[j]} \sim dnorm(\mu.\psi 0_{landuse[j]}, \sigma^2.\psi 0_{landuse[j]})$$

and

$$\psi 1_{i,landuse[j]} \sim dnorm(\mu.\psi 1_{landuse[j]}, \sigma^2.\psi 1_{landuse[j]})$$

This parameterization corresponds to a fixed intercept and rainfall slope in each land-use, with random species intercepts and slopes generating species-specific responses. Finally $\psi 2_{i,j}$ represents residual random effects to account for species-specific variation among sites in occupancy levels. $\psi 2_{i,j}$ was drawn from a normal distribution with mean 0, and standard deviation $\sigma^2.\psi 2$.

Similarly the detection component is parameterized according to:

$$logit(p_{i,j,t,k}) = p0_{landuse[j]} + p1_i + p2_j + p3_t + p4_{i,j,t},$$

With terms defined equivalently to those in the dynamic model above.

iii) Multispecies occupancy model to obtain habitat affiliation scores

Here, we modeled occupancy for each species *i* at each site *j* in each year *t* directly from the data. Our focus was on parameterizing the model such the individual parameter estimates represented each species' preference for agricultural habitats versus forest.

$$logit(\psi_{i,j,t}) = \psi 0_{i,region[j]} + \psi 1_{i,landuse[j]} + \psi 2_{i,j}$$

$\psi 0$ allows each species to have a unique average occupancy in each region (due to full parameterization of the model, this term is interpreted as the expected occupancy of a species in forest). In each region, individual species were drawn from region-specific normal distribution with independent means and variance terms (species specific random intercepts for each region).

$$\psi 0_{i,region[j]} \sim Norm(\mu.\psi 0_{region[j]}, \sigma^2.\psi 0_{region[j]})$$

$\psi 1$ describes the species-specific contrast in occupancy versus forest. For all species, $\psi 1$ in forest was set to 0 ($\psi 0_{i,j} = 0$). For the other two land-use types, species were drawn from a land-use specific distribution characterized by distinct mean and variance terms (species-specific random contrast of land-use). Specifically for sites in diversified and intensive agriculture:

$$\psi 1_{i,j} \sim Norm(\mu.\psi 1_{landuse[j]}, \sigma^2.\psi 1_{landuse[j]})$$

Final $\psi 2_{i,j}$ absorbs residual species-specific variation for each site.

$$\psi 2_{i,j} \sim Norm(0, \sigma^2_{\psi 2})$$

Detection probability was parameterized as above:

$$logit\left(p_{i,j,t,k}\right) = p0_{landuse[j]} + p1_i + p2_j + p3_t + p4_{i,j,t},$$

Models were run and convergence verified, as above.

iii) Agriculture affiliation metric

We used the occupancy model (above) to calculate habitat affinity for each species. By setting the family of parameters of $\psi1_{i,Forest}$ equal to zero, the resulting estimates for $\psi1_{i,Diversified\ Ag}$ and $\psi1_{i,Intensive\ Ag}$ represent the degree to which species *i* achieves higher (or lower) occupancy in agriculture, relative to forest. Because variation between regions and individual sites was captured by $\psi0$ and $\psi2$, values of $\psi1$ represent an appropriate and directly estimatable metric of habitat affinity: the log odds of a given species occupying the focal agricultural habitat versus forest. Because the contrast between forest and diversified agriculture and forest and intensive agriculture were highly correlated (R = 0.88 and 0.86 for dry and wet season respectively), we averaged the parameter estimates $\psi1_{i,Diversified\ Ag}$ and $\psi1_{i,Intensive\ Ag}$ for each species *i* to derive an overall agriculture affiliation.

Climate and Land-use SDMs and Range Size Projections

SDMs presented in the main text only included climate variables to estimate distributions and project those distributions into the future. However, because climate is not the only feature limiting species ranges these estimates may not reflect reality. In particular, even if a local climate regime is favorable for a species, land-use characteristics may make certain areas inhospitable, or alternatively, make otherwise inhospitable areas viable. To verify that changes in land-use did not confound our climate predictions, we parameterized a second series of SDMs with the same climate variables as well as 5 land-use variables extracted from the Land-use Harmonization project (natural primary habitat, secondary successional habitat, cropland, pasture land, and urban) (Hurtt *et al.* 2011). Specifically, we quantified each land-use variable as its proportional coverage within each grid cell. Low-resolution land-use data cannot be tied to individual detections, however, these data do provide some insight into land-use preferences, as they allow for probabilistic sampling of the land covers in regions where each species is most frequently found.

After building SDMs that predicted current species distributions from land-use and climate data, we projected future species distributions in two ways. First, we allowed both climate and land-use to change, using land-use models for 2070 for each RCP scenario obtained from the Land-use Harmonization project (Hurtt *et al.* 2011). Second, we allowed climate to change, but held land-use constant in current conditions. This second case in effect controls for land-use change, demonstrating that differences in species range sizes in the future are indeed due to climate change, rather than correlations between present day climate and land-use.

Comparing the full suite of scenarios in which land-use was allowed to vary, held constant over time, and omitted from models entirely allowed for evaluation of the robustness of our findings to assumptions regarding how species respond to climate versus land-use change.

References in Supplement

Carrillo-Rubio, E., Kéry, M., Morreale, S.J., Sullivan, P.J., Gardner, B., Cooch, E.G., *et al.* (2014). Use of multispecies occupancy models to evaluate the response of bird communities to forest degradation associated with logging. *Conserv. Biol.*, 28, 1034–1044.

Gelman, A. & Hill, J. (2007). *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York.

Hurtt, G.C., Chini, L.P., Frolking, S., Betts, R. a., Feddema, J., Fischer, G., *et al.* (2011). Harmonization of land-use scenarios for the period 1500-2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Clim. Change*, 109, 117–161.

Simard, M., Pinto, N., Fisher, J.B. & Baccini, A. (2011). Mapping forest canopy height globally with spaceborne lidar. *J. Geophys. Res. Biogeosciences*, 116, 1–12.

Supplementary Figures and Tables

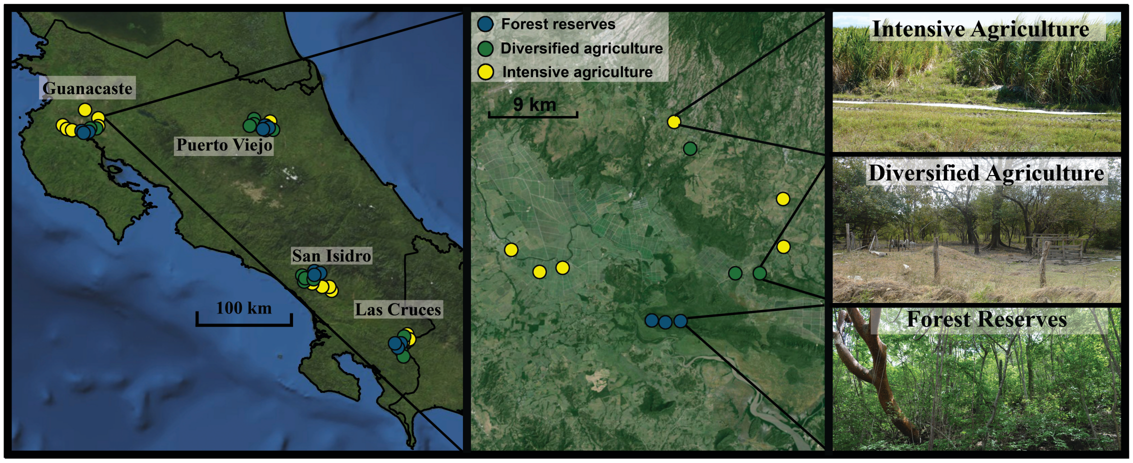


Fig. S1: Map of study sites. Left panel depicts survey transects (colored points) in four study regions (Guanacaste, Puerto Viejo, San Isidro, and Las Cruces). Middle panel depicts survey transects in one study region (Guanacaste). Points are colored according to land use (blue = forest reserves; green = diversified agriculture; yellow = intensive agriculture). Right panels show photos from each land use type.

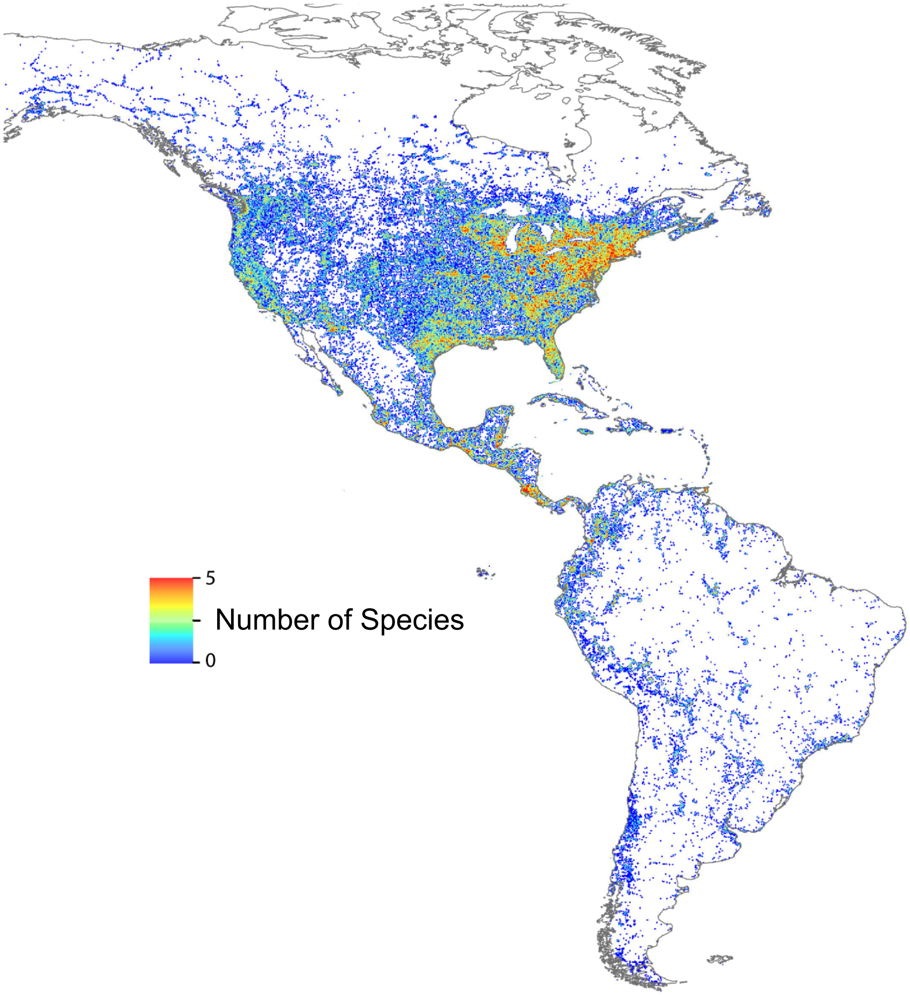


Fig. S2: Number of species with observation data within each 10km^2 grid cell across North and South America. These presence data were used to develop species distribution models for 307 species included in the study.

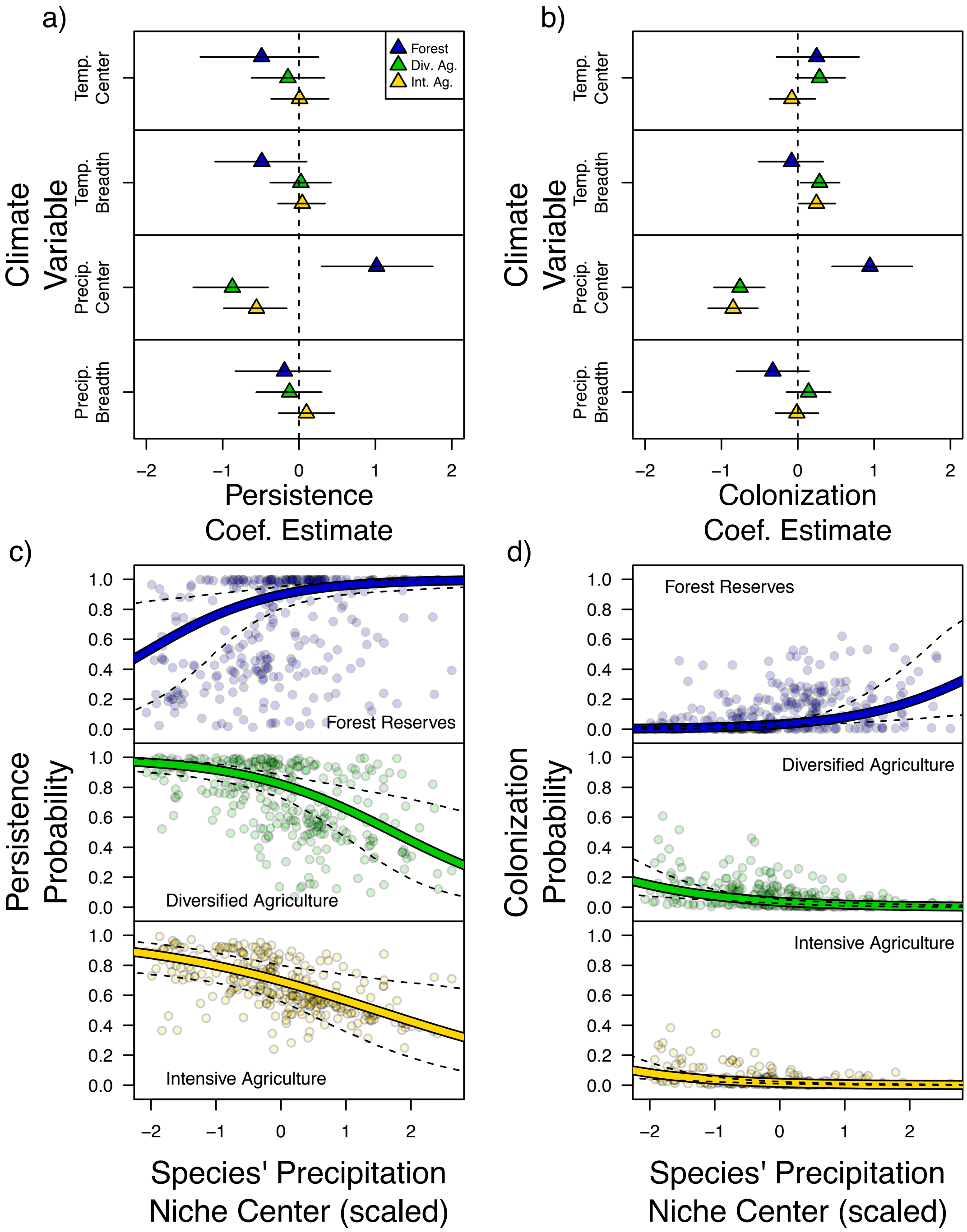


Fig. S3. Occupancy parameters during dry season. a-b) Summary of parameter estimates for the effects of species' climatological niche characteristics on persistence and colonization rates in forest (dark blue), diversified agriculture (green), and intensive agriculture (yellow). Points depict posterior means, and lines show 95% Bayesian credible intervals. c-d) Posterior estimates of persistence and colonization rates for all 307 bird species in each of the three investigated land uses depicting the effect of species' precipitation niche center from the dry-season sample. Species from drier climates persisted and colonized agriculture better than species from wet climates, while the converse was true in forest. Points represent posterior means for each species, while the best-fit line represents the expectation based on the posterior means of parameters governing how precipitation niche influences persistence and colonization probabilities, with dashed lines indicating 95% BCIs.

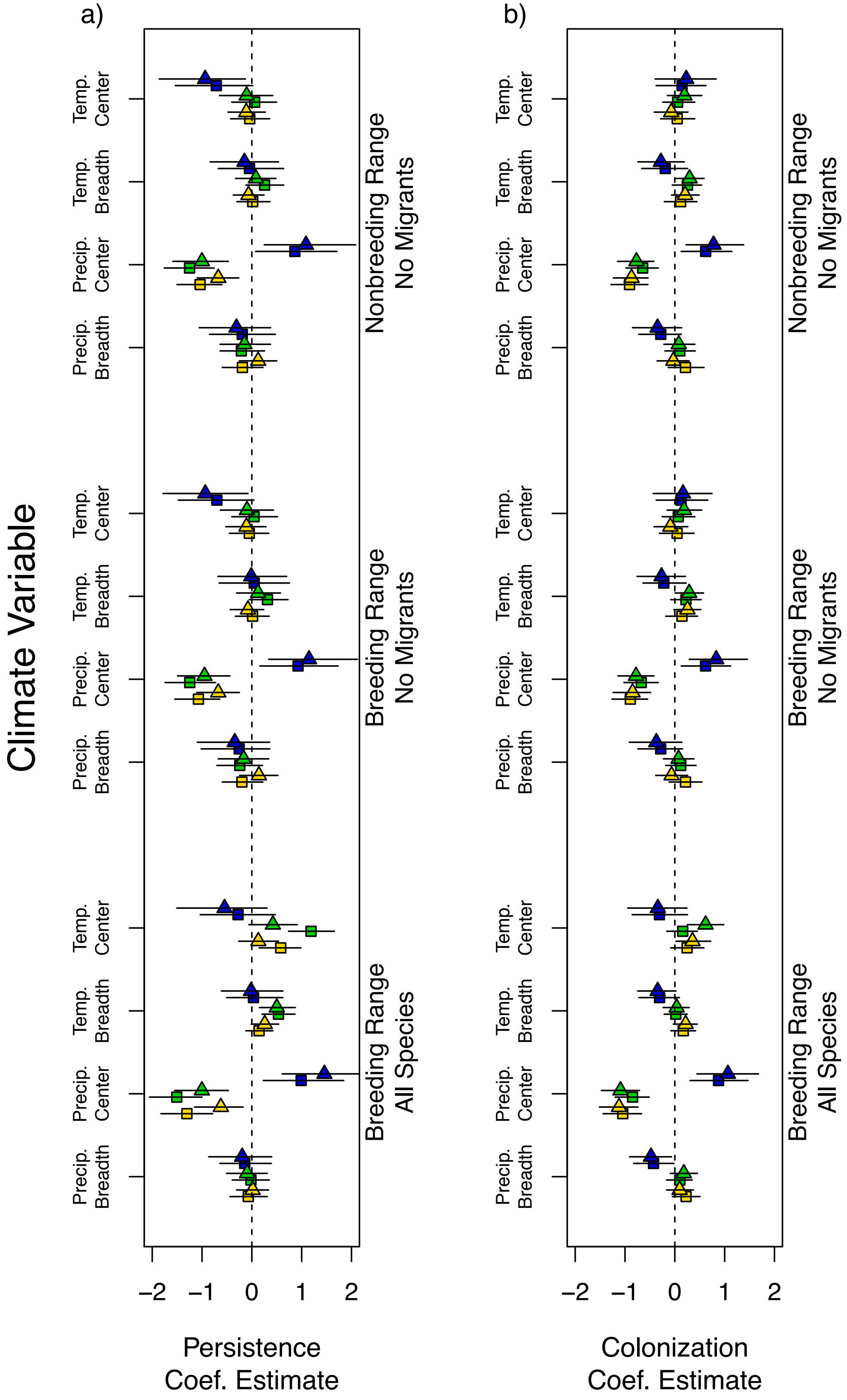

a)
b)
Climate Variable
Temp. Center
Temp. Breadth
Precip. Center
Precip. Breadth
Nonbreeding Range No Migrants
Breeding Range No Migrants
Breeding Range All Species
−2
−1
0
1
2
Persistence Coef. Estimate
Colonization Coef. Estimate

Figure S4. Summary of parameter estimates for the effects of species' climatological niche characteristics on persistence (a) and colonization rates (b) in forest (dark blue), diversified agriculture (green), and intensive agriculture (yellow). Triangles indicate dry season estimates, while squares depict wet season estimates. Points are posterior means, and lines show 95% Bayesian credible intervals. Parameter estimates for the wet and dry season for Nonbreeding season ranges for all bird species are depicted in figures 1 and S2. Across all data partitions only precipitation niche consistently explains habitat affiliation with forest and agriculture.

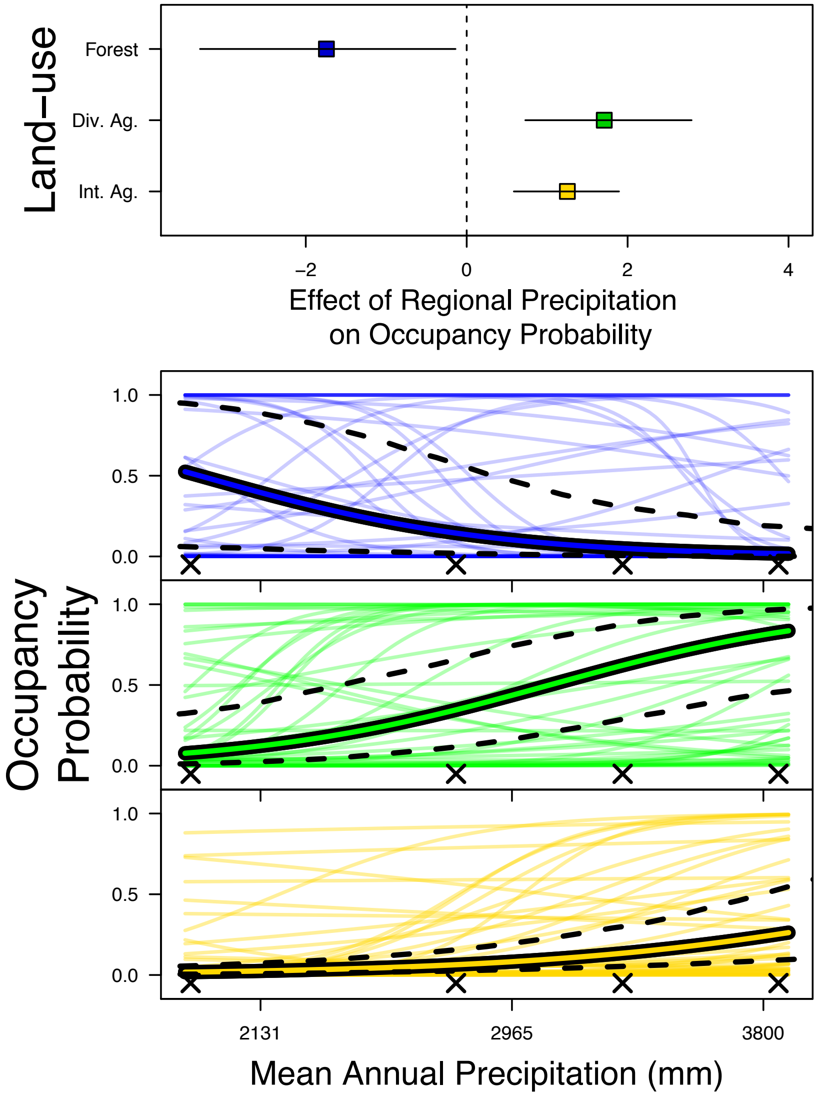


Figure S5: Habitat shifting among the 47 species encountered in all study regions in the dry season sample. Contrast with wet season sample presented in the main text (Figure 2). Top panel depicts the effect of regional rainfall on species' occupancy in each habitat type (posterior mean +/- 95% Bayesian credible interval). The bottom panel shows overall occupancy probability across the rainfall gradient. Large lines depict mean effects across species in each habitat (forest=blue, div. ag. = green, int. ag. = yellow), while thin lines show responses of each of the 47 individual species, based on fitted multispecies occupancy model. Rainfall in each of the four regions is indicated by an 'X'.

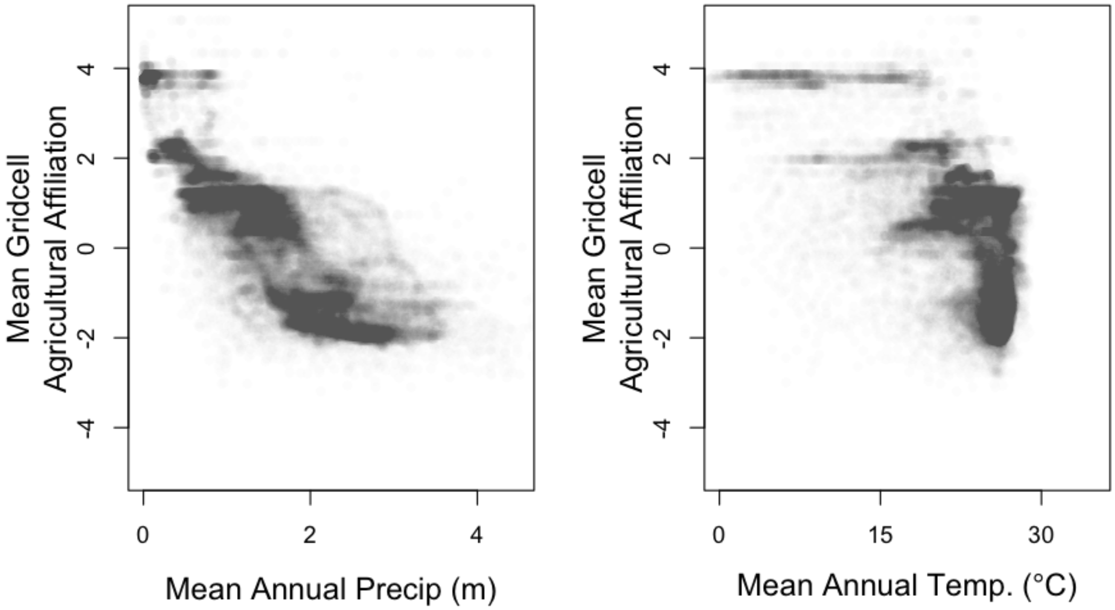
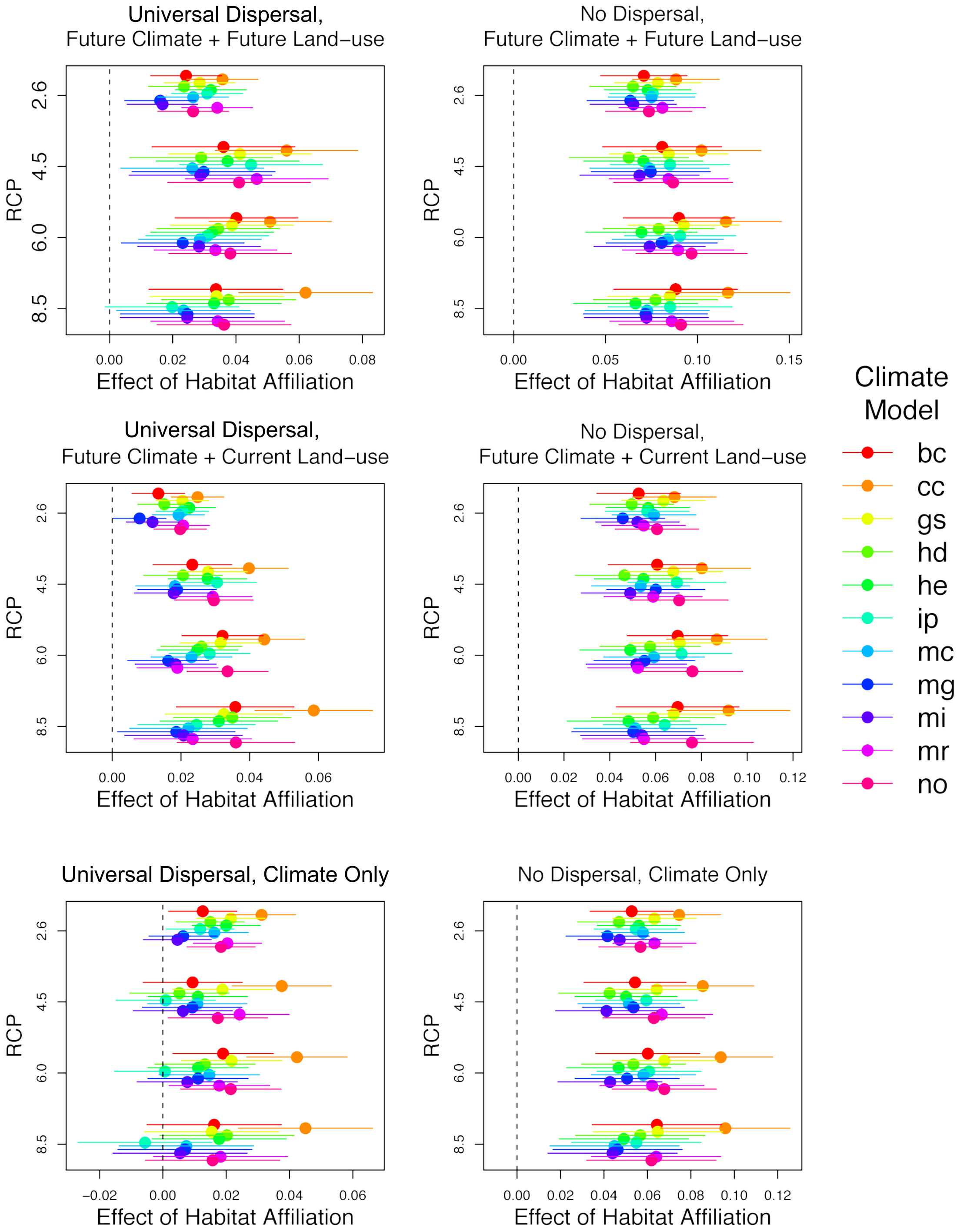


Figure S6: Correlation between mean annual precipitation or mean annual temperature across the tropics with the average agricultural affiliation of Costa Rican species that occur there. Each semi-transparent black point represents a 1/3 degree by 1/3 degree grid cell.


Universal Dispersal, Future Climate + Future Land−use

No Dispersal, Future Climate + Future Land−use

Universal Dispersal, Future Climate + Current Land−use

No Dispersal, Future Climate + Current Land−use

Universal Dispersal, Climate Only

No Dispersal, Climate Only

Figure S7: Agricultural affiliated species tend to be more resistant to future climate change regardless of assumptions regarding dispersal. Points indicate maximum likelihood parameter estimates explaining how habitat affiliation will affect a species' expected range expansion (positive values indicate agricultural affiliation is positively correlated with future range size). Lines represent 95% profile-likelihood CI. Species distribution models were generated for species based on current climate conditions and current land-use information, or based on climate data only. Then each species range across the western hemisphere was quantified under future conditions across the four RCP scenarios and using 11 climate circulation models. For SDMs generated with both land-use and climate data future scenarios included either both future climate and future land-use, or future climate but holding land use at present day conditions to isolate the effects of climate change. For SDMs generated with just climate data only future climate conditions were used. Species were either assumed to be able to disperse and colonize any area in the western hemisphere where habitat was suitable (Universal Dispersal), or were assumed to be unable to disperse beyond the area they currently occupy (No Dispersal). For each RCP models were run with full interaction fixed effects of 'habitat affiliation' and 'climate model', with a random intercept of species to account for non-independence of species identity across climate models.

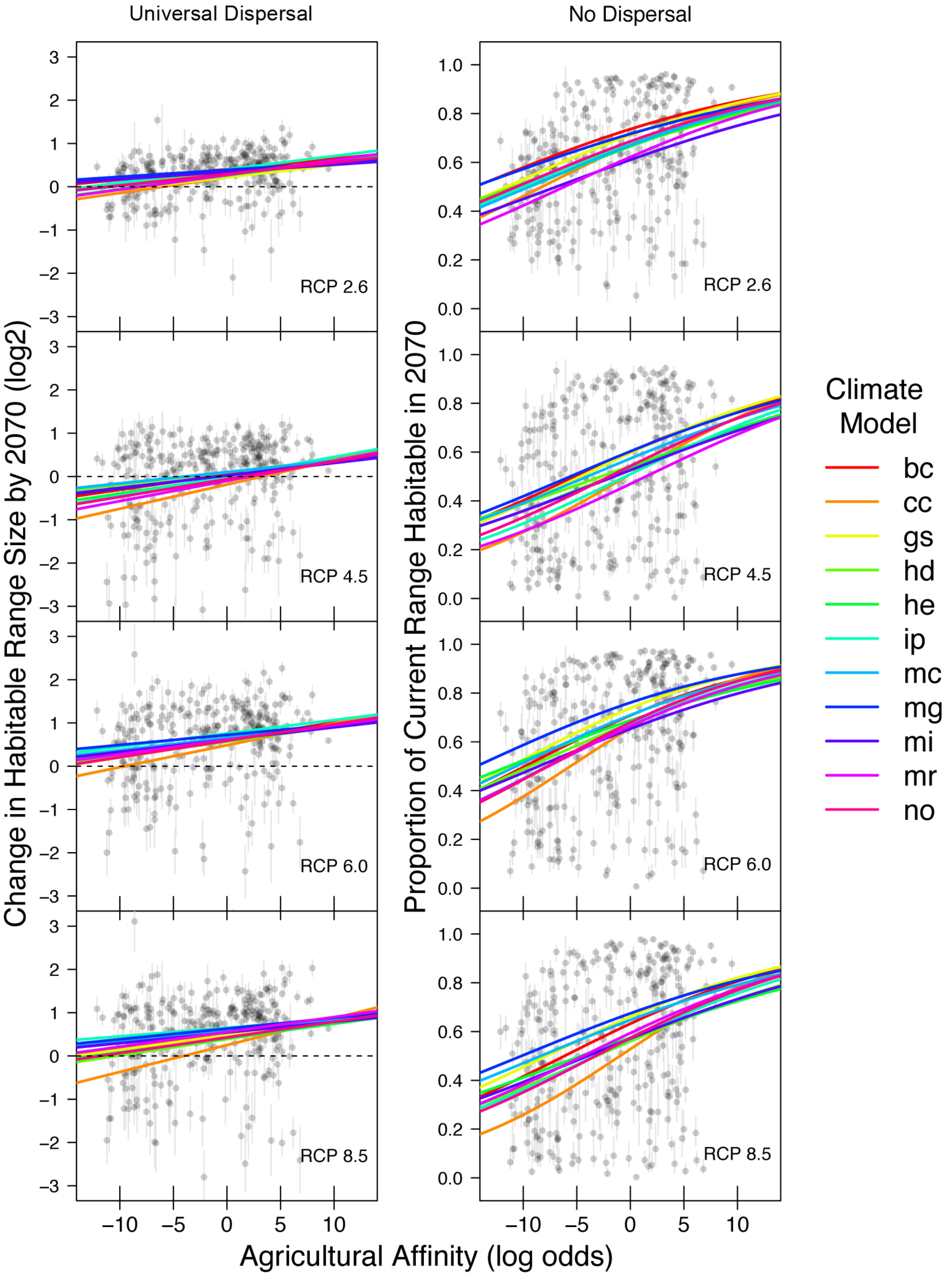


Figure S8: Full data plots for SDMs based on current climate and land-use data, and projected using into the future using both future climate and land-use data. Agricultural affiliated species on average either increase in their habitable range, or suffer less range loss under future climate change. See figure S6 for presentation of alternative SDM assumptions affect slope parameter estimates.

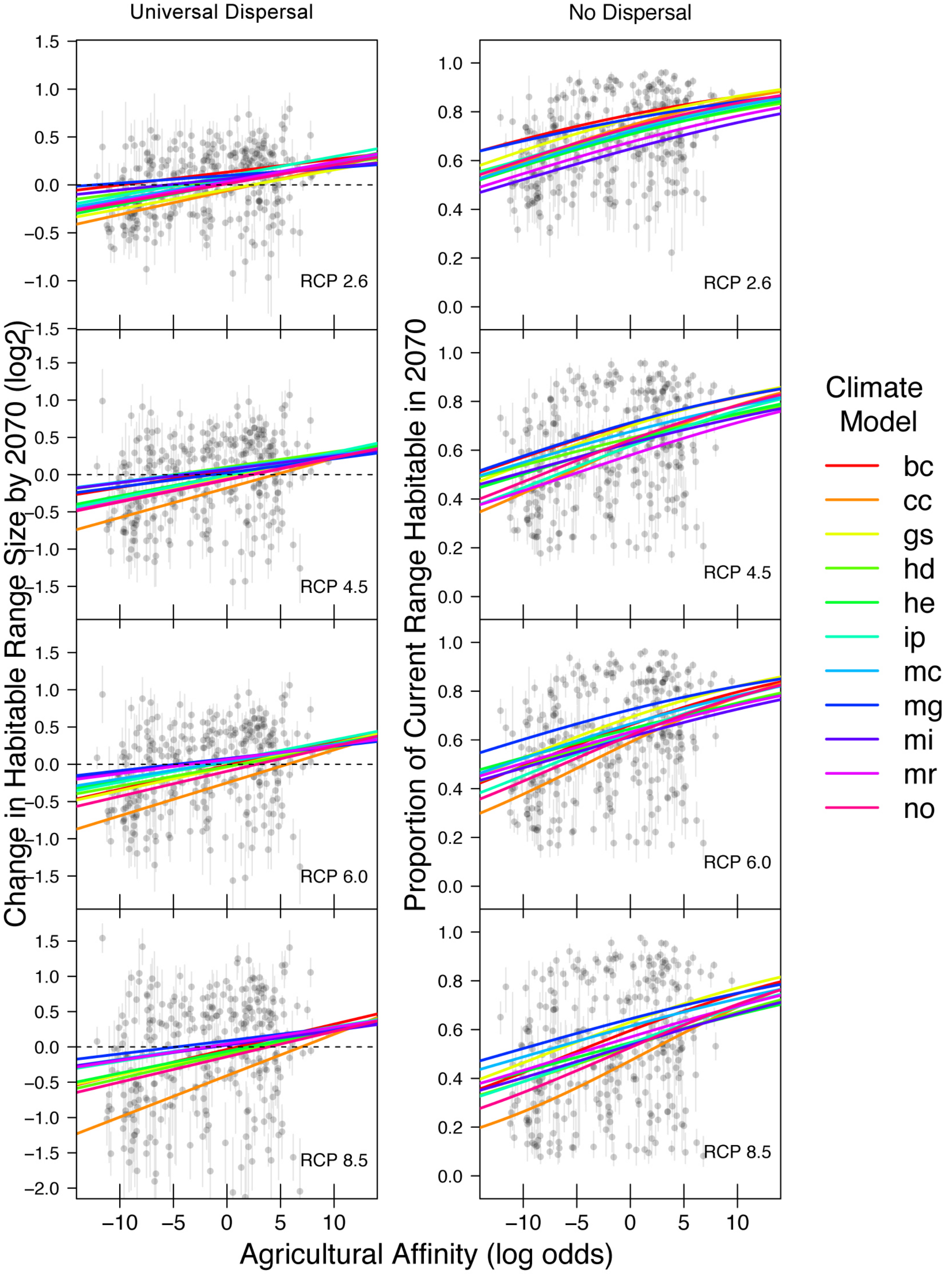


Figure S9: Full data plots for SDMs based on current climate and land-use data, and projected using into the future using future climate but current land-use data to isolate the effect of climate change on shifts in habitable range size. See figure S6 for presentation of alternative SDM assumptions affect slope parameter estimates.

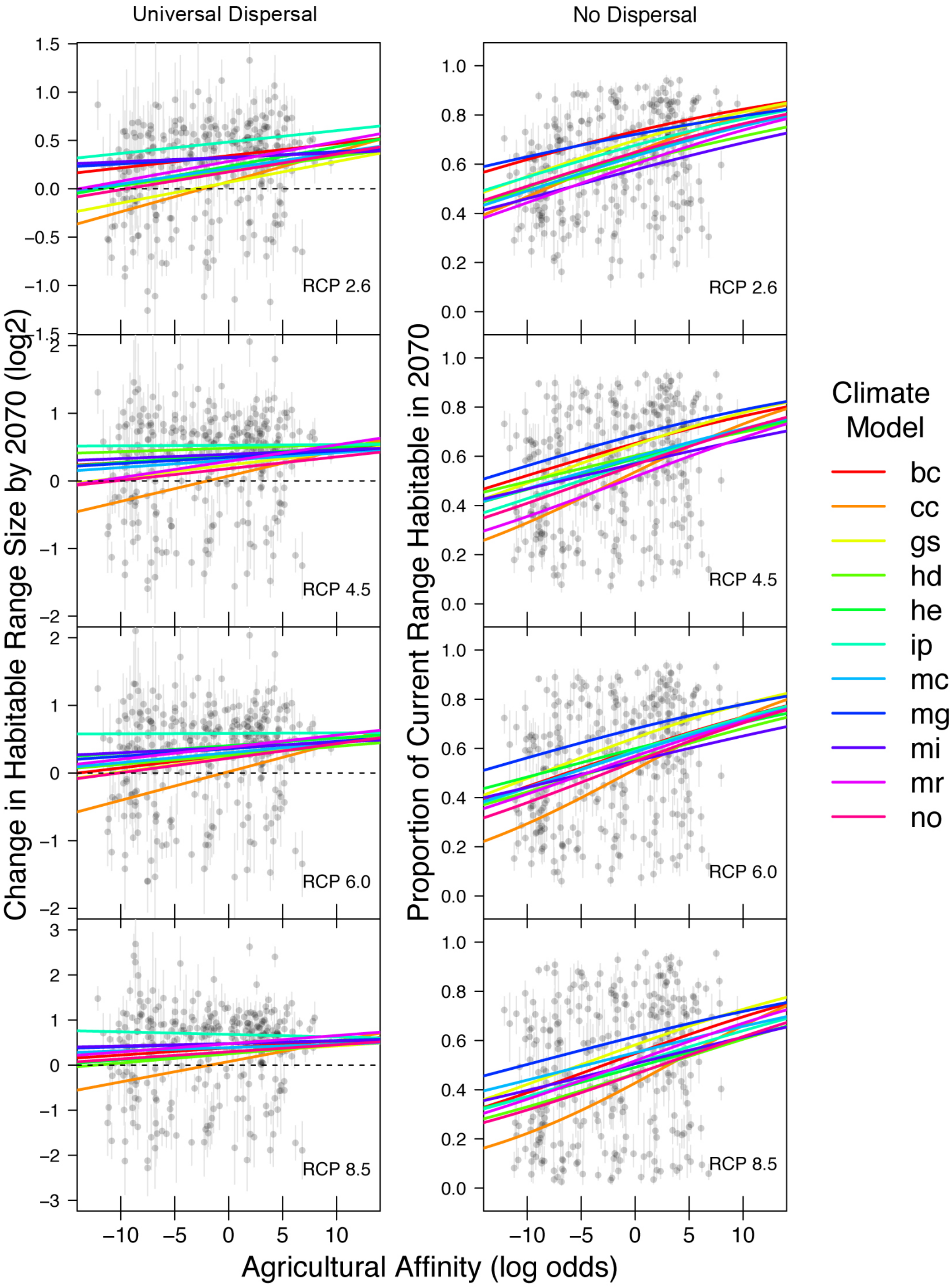


Figure S10: Full data plots for SDMs based on current climate data only, and projected into the future using future climate data. See figure S6 for presentation of alternative SDM assumptions affect slope parameter estimates.

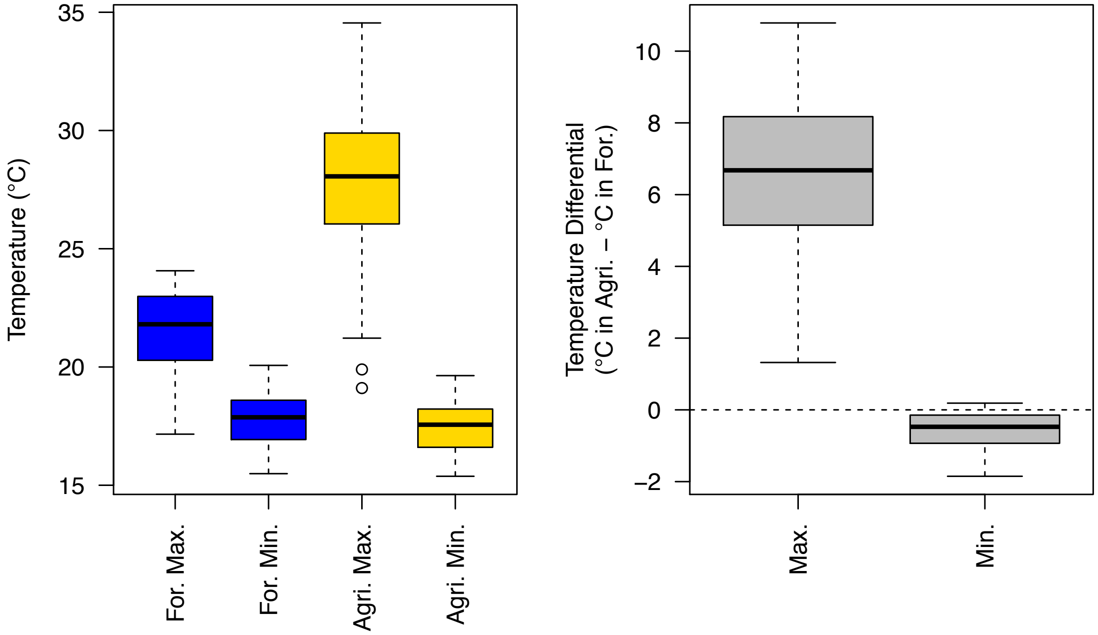


Figure S11: Temperature conditions from three adjacent forest and agricultural sites in Las Cruces region during 2011. Left hand plot depicts the distribution of daily maxima and minima in forest and agriculture, pooling all three sites ($N_{\text{site-days}}$ = 76). Right hand side presents temperature differential of both daily maxima and minima between paired sites, indicating how much warmer agricultural sites are than the forested sites. Note that these sites were different from those used to sample bird communities, and are included to illustrate general differences between tropical forest and agriculture.

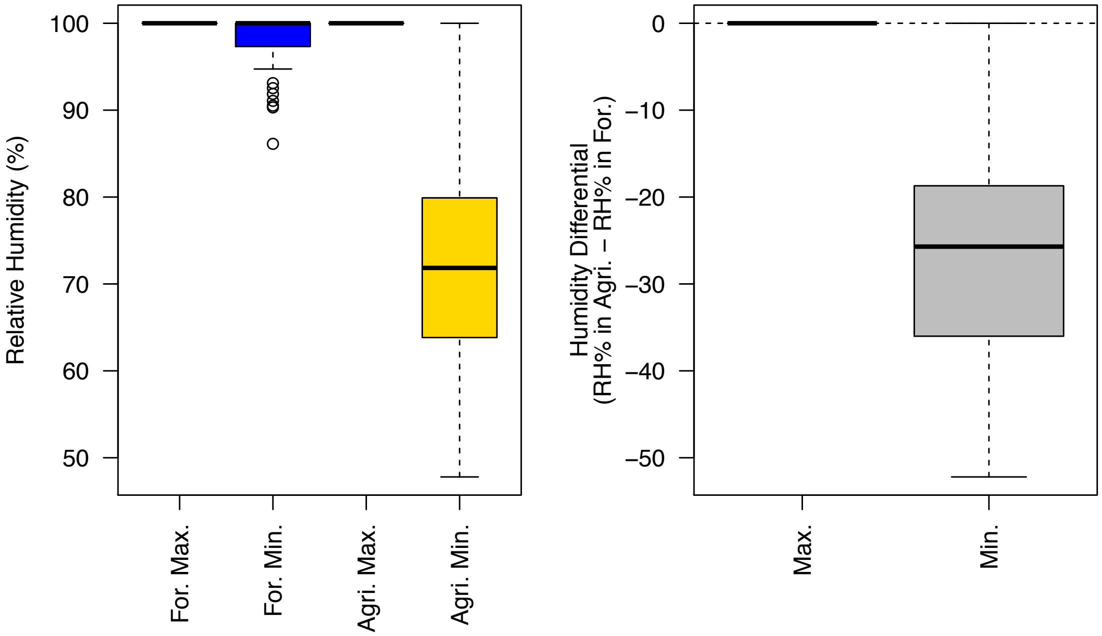


Figure S12: Humidity conditions from three adjacent forest and agricultural sites in Las Cruces region during 2011. Left hand plot depicts the distribution of daily maxima and minima in forest and agriculture, pooling all three sites ($N_{\text{site-days}} = 76$). Right hand side presents relative humidity differential of both daily maxima and minima between paired sites, indicating how much drier agricultural sites are than the forested sites. Note that these sites were different from those used to sample bird communities, and are included to illustrate general differences between tropical forest and agriculture.

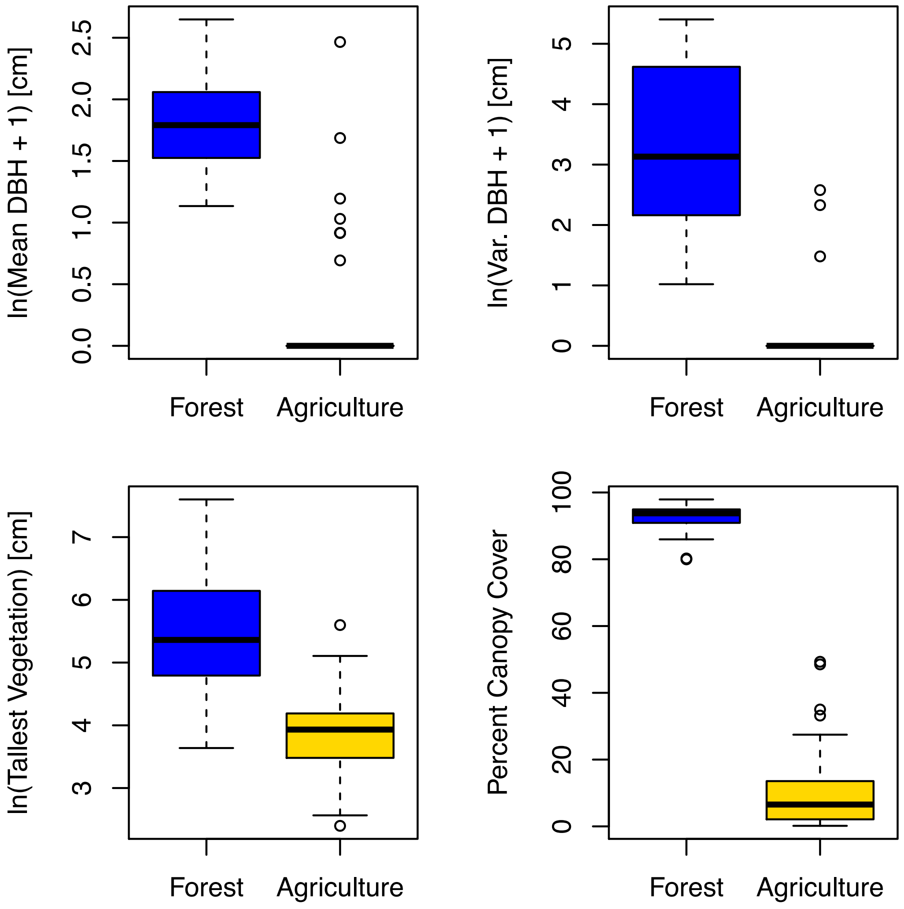


Figure S13: Representative differences in vegetation from 90 forest and agricultural 1 meter-square plots in and around the Las Cruces region. Data are from 30 elevational transect sites from Frishkoff *et al.* (2015). Agricultural sites possess less vegetative structure as indicated by the mean diameter at breast height (DBH) of woody plants within the plot, the variance of DBHs within the plot, the maximum vegetation height within the plot, and the degree to which the plot was covered by a canopy, as measured by a spherical densiometer. Note that these sites were different from those used to sample bird communities, and are included to illustrate general differences between tropical forest and agriculture.

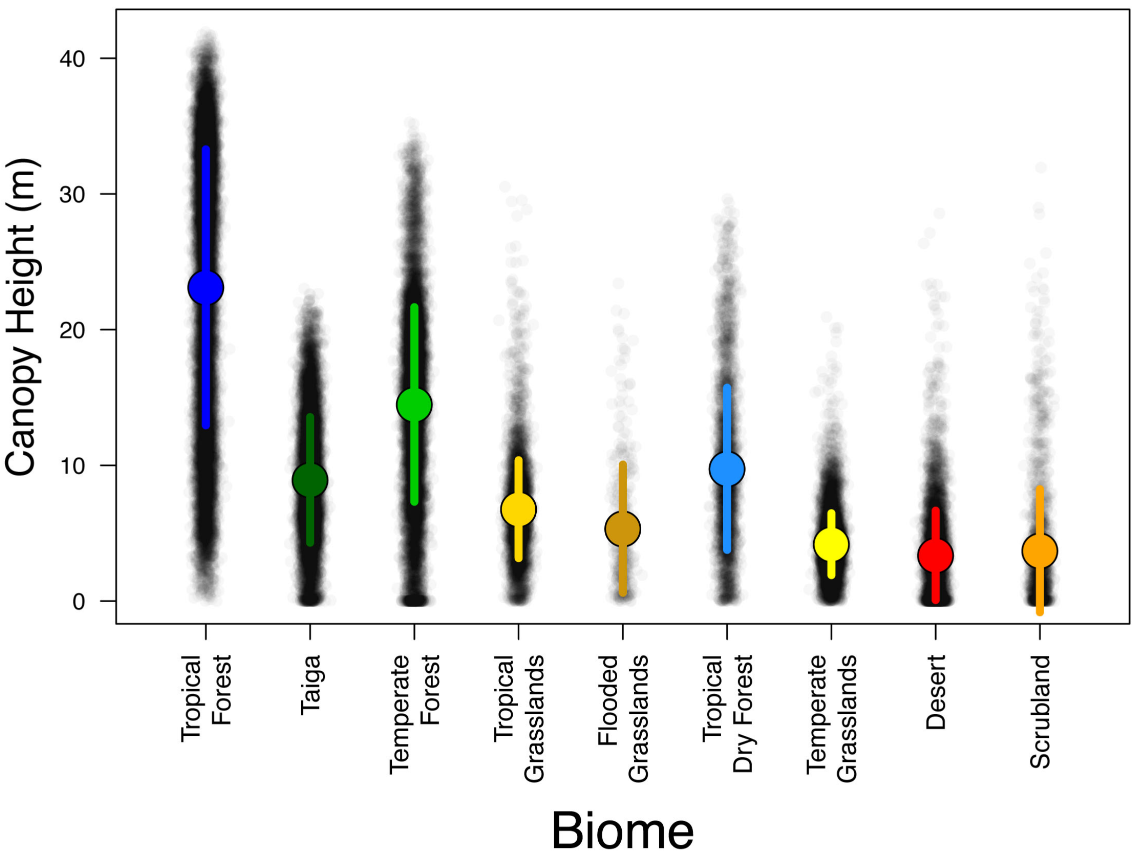


Figure S14: Average canopy height from 3D Global Vegetation Map Database (Simard *et al.* 2011) for each grid cell in the major biomes in North and South America. Biomes are order according to average habitat affiliation of Costa Rican bird species (as in figure 3 in the main text). Dry biomes, where Costa Rica's agricultural species are more likely to come from have shorter vegetation structure. Small semi-transparent black points represent individual grid cells, large colored points are means of the distribution, while lines represent standard deviation of the data.

Table S1: Summary of regions indicating the general location each region occupies in the country, whether it is on the Atlantic or Pacific versant, and a description of the natural and agricultural habitat available for species.

Region	Area	Versant	Natural Vegetation	Major Agriculture
Guanacaste	Northwestern Costa Rica	Pacific Versant	Lowland tropical dry forest	Melon, rice, sugar cane, cattle, and aquaculture
San Isidro	South-Central Costa Rica	Pacific Versant	Mid-elevation tropical wet forest	Coffee, pineapple, sugar cane, pasture
Las Cruces	Southern Costa Rica	Pacific Versant	Premontane tropical wet forest	Coffee, pasture
Puerto Viejo	Northern Costa Rica	Atlantic Versant	Lowland tropical wet forest	Heart-of-palm, banana, pineapple, pasture

Table S2: Structural differences between diversified agriculture and intensive monocultures. Values are means (SD) across transects from surveys conducted in 1999. Table adapted from (Karp et al. 2012).

	Vegetation Variable	Diversified Agriculture	Intensive Agriculture
Crop Diversity	Number of planted crop species	21.4 (12.8)	4.5 (2.9)
Hedgerow Quality and Extent	% without hedgerows	48.5 (26.6)	69.7 (35.1)
	% short & thin hedgerows	6.2 (5.6)	5.5 (12.1)
	% short & full hedgerows	7.5 (10.3)	9.2 (24.8)
	% tall & thin hedgerows	26.6 (19)	11.6 (18.5)
	% tall & full hedgerows	11.2 (12.4)	3.7 (6.8)
Agricultural plot structure	Plot size (hectares)	3.3 (7.6)	65.5 (78.7)
	Number of bordering plots	6.3 (3.9)	1.9 (1.1)
Forest cover	% forest cover at 100m buffer	7 (21)	1 (4)
	% forest cover at 200m buffer	10 (21)	2 (6)

Table S3: Table of all parameter estimates from dynamic occupancy models. ‘Posterior’ presents posterior means [2.5%, 97.5% BCI], and ‘Prior’ indicates the prior distribution from which the parameters were drawn.

Hierarchy	**Parameter**	**Description**	**Posterior**	**Prior**
Occupancy – Persistence	μ.φ0 [forest]	Mean of spp in forest (Guanacaste)	2.165 [1.349, 3.01]	logit(U[0,1])
	μ.φ0 [intensive]	Mean of spp in intensive (Guanacaste)	0.92 [0.344, 1.505]	logit(U[0,1])
	μ.φ0 [diversified]	Mean of spp in diversified (Guanacaste)	1.542 [0.869, 2.225]	logit(U[0,1])
	μ.φ1[Las Cruces]	Mean region contrast (Las Cruces)	-0.037 [-0.846, 0.733]	N(0, 1000)
	μ.φ1[Puerto Viejo]	Mean region contrast (Puerto Viejo)	-0.208 [-1.032, 0.618]	N(0, 1000)
	μ.φ1[San Isidro]	Mean region contrast (San Isidro)	-0.458 [-1.269, 0.266]	N(0, 1000)
	σ.φ0 [forest]	SD of species in forest	3.516 [2.777, 4.471]	U(0,20)
	σ.φ0 [intensive]	SD of species in intensive	1.368 [1.038, 1.719]	U(0,20)
	σ.φ0 [diversified]	SD of species in diversified	2.041 [1.689, 2.433]	U(0,20)
	σ.φ1[Las Cruces]	SD region contrast across spp (Las Cruces)	2.058 [1.689, 2.444]	U(0,20)
	σ.φ1[Puerto Viejo]	SD region contrast across spp (Puerto Viejo)	2.446 [2.036, 2.933]	U(0,20)
	σ.φ1[San Isidro]	SD region contrast across spp (San Isidro)	1.943 [1.549, 2.396]	U(0,20)
	σ.φ6	SD of site random effect	0.699 [0.49, 0.946]	U(0,5)
	φ2[forest]	Effect of temp. center in forest	-0.415 [-1.101, 0.225]	N(0, 1000)
	φ2[intensive]	Effect of temp. center in intensive	0.057 [-0.322, 0.41]	N(0, 1000)
	φ2[diversified]	Effect of temp. center in diversified	0.212 [-0.232, 0.675]	N(0, 1000)
	φ3[forest]	Effect of temp. breadth in forest	-0.413 [-0.981, 0.125]	N(0, 1000)
	φ3[intensive]	Effect of temp. breadth in intensive	0.13 [-0.174, 0.418]	N(0, 1000)
	φ3[diversified]	Effect of temp. breadth in diversified	0.03 [-0.327, 0.41]	N(0, 1000)
	φ4[forest]	Effect of precip. center in forest	0.708 [0.049, 1.424]	N(0, 1000)
	φ4[intensive]	Effect of precip. center in intensive	-1.009 [-1.456, -0.563]	N(0, 1000)
	φ4[diversified]	Effect of precip. center in diversified	-1.23 [-1.744, -0.789]	N(0, 1000)
	φ5[forest]	Effect of precip. breadth in forest	-0.165 [-0.728, 0.377]	N(0, 1000)
	φ5[intensive]	Effect of precip. breadth in intensive	-0.102 [-0.482, 0.277]	N(0, 1000)
	φ5[diversified]	Effect of precip. breadth in diversified	-0.135 [-0.549, 0.276]	N(0, 1000)
Occupancy - Colonization	μ.γ0 [forest]	Mean of spp in forest (Guanacaste)	-3.232 [-3.832, -2.637]	logit(U[0,1])
	μ.γ0 [intensive]	Mean of spp in intensive (Guanacaste)	-4.18 [-4.641, -3.709]	logit(U[0,1])
	μ.γ0 [diversified]	Mean of spp in diversified (Guanacaste)	-3.287 [-3.8, -2.718]	logit(U[0,1])
	μ.γ1[Las Cruces]	Mean region contrast (Las Cruces)	0.233 [-0.37, 0.801]	N(0, 1000)
	μ.γ1[Puerto Viejo]	Mean region contrast (Puerto Viejo)	0.07 [-0.481, 0.628]	N(0, 1000)
	μ.γ1[San Isidro]	Mean region contrast (San Isidro)	-0.067 [-0.616, 0.511]	N(0, 1000)
	σ.γ0 [forest]	SD of species in forest	2.642 [2.193, 3.176]	U(0,20)
	σ.γ0 [intensive]	SD of species in intensive	1.565 [1.317, 1.835]	U(0,20)
	σ.γ0 [diversified]	SD of species in diversified	1.474 [1.232, 1.744]	U(0,20)
	σ.γ1[Las Cruces]	SD region contrast across spp (Las Cruces)	1.126 [0.892, 1.411]	U(0,20)
	σ.γ1[Puerto Viejo]	SD region contrast across spp (Puerto Viejo)	0.989 [0.748, 1.266]	U(0,20)

	*σ.*γ1[San Isidro]	SD region contrast across spp (San Isidro)	1.326 [1.072, 1.607]	U(0,20)
	*σ.*γ6	SD of site random effect	0.566 [0.427, 0.743]	U(0,5)
	γ2[forest]	Effect of temp. center. in forest	0.314 [-0.204, 0.81]	N(0, 1000)
	γ2[intensive]	Effect of temp. center. In intensive	0.012 [-0.309, 0.321]	N(0, 1000)
	γ2[diversified]	Effect of temp. center. In diversified	0.119 [-0.182, 0.409]	N(0, 1000)
	γ3[forest]	Effect of temp. breadth in forest	-0.077 [-0.471, 0.326]	N(0, 1000)
	γ3[intensive]	Effect of temp. breadth in intensive	0.29 [0.039, 0.547]	N(0, 1000)
	γ3[diversified]	Effect of temp. breadth in diversified	0.353 [0.1, 0.613]	N(0, 1000)
	γ4[forest]	Effect of precip center. in forest	0.756 [0.293, 1.234]	N(0, 1000)
	γ4[intensive]	Effect of precip center. In intensive	-0.801 [-1.125, -0.485]	N(0, 1000)
	γ4[diversified]	Effect of precip center. In diversified	-0.609 [-0.911, -0.298]	N(0, 1000)
	γ5[forest]	Effect of precip breadth in forest	-0.253 [-0.67, 0.158]	N(0, 1000)
	γ5[intensive]	Effect of precip breadth in intensive	0.166 [-0.122, 0.456]	N(0, 1000)
	γ5[diversified]	Effect of precip breadth in diversified	0.119 [-0.141, 0.37]	N(0, 1000)
Detection	μ.p0[forest]	Mean detection in forest	-0.701 [-1.036, -0.368]	logit(U[0,1])
	μ.p0[intensive]	Mean detection in intensive	-1.333 [-1.646, -1.004]	logit(U[0,1])
	μ.p0[diversified]	Mean detection in diversified	-0.778 [-1.104, -0.453]	logit(U[0,1])
	σ.p1	SD of random spp effect	1.428 [1.306, 1.562]	U(0,10)
	σ.p2	SD of random site effect	0.498 [0.37, 0.652]	U(0,5)
	σ.p3	SD of random year effect	0.113 [0.066, 0.199]	U(0,5)
	σ.p4	SD of random site X year X spp effect	0.975 [0.936, 1.018]	U(0,5)

Appendix 1: Dynamic Occupancy model for climate variables

```
model.jags<-function() {

    ## ******************************************************
    ## Detection Priors
    ## ******************************************************

    for (int in 1:3){
      p.intensity.pre[int] ~ dunif(0,1)
      p.intensity[int] <- logit(p.intensity.pre[int])
    }

    for (site in 1:nsite) {
      p.site[site] ~ dnorm(0, tau.p.site)
    }

    for (yr in 1:nyear) {
      p.year[yr] ~ dnorm(0, tau.p.yr)
    }

    sigma.p.0 ~ dunif(0,100)
    tau.p.0 <- 1/(sigma.p.0*sigma.p.0)

    sigma.p.yr ~ dunif(0,5)
    tau.p.yr <- 1/(sigma.p.yr*sigma.p.yr)

    sigma.p.site ~ dunif(0,5)
    tau.p.site <- 1/(sigma.p.site*sigma.p.site)

    sigma.p.site.yr.sp ~ dunif(0,5)
    tau.p.site.yr.sp <- 1/(sigma.p.site.yr.sp*sigma.p.site.yr.sp)


    ## ******************************************************
    ## Occupancy priors (phi = persistence, gam = colonization)
    ## ******************************************************
    ## Random site effects

    sigma.phi.site ~ dunif(0,5)
    sigma.gam.site ~ dunif(0,5)
    tau.phi.site <- 1/(sigma.phi.site* sigma.phi.site)
    tau.gam.site <- 1/(sigma.gam.site* sigma.gam.site)

    for (site in 1:nsite){
      phi.site[site] ~ dnorm(0, tau.phi.site)
      gam.site[site] ~ dnorm(0, tau.gam.site)
    }

    ## Generate mean and sd of species occupancies in each land-use
    for(i in 1:3) {
      mu.phi.intensity.pre[i] ~ dunif(0,1)
      mu.gam.intensity.pre[i] ~ dunif(0,1)
```

```
  mu.phi.intensity[i] <- logit(mu.phi.intensity.pre[i])
  mu.gam.intensity[i] <- logit(mu.gam.intensity.pre[i])

  sigma.phi.intensity[i] ~ dunif(0,20)
  sigma.gam.intensity[i] ~ dunif(0,20)

  tau.phi.intensity[i]<-1/(sigma.phi.intensity[i] * sigma.phi.intensity[i])
  tau.gam.intensity[i]<-1/(sigma.gam.intensity[i] * sigma.gam.intensity[i])

}

## Draw each species land-use responses
for(sp in 1:nsp){
   for (i in 1:3) {
      phi.intensity.sp[i,sp] ~ dnorm(mu.phi.intensity[i],
                                       tau.phi.intensity[i])
      gam.intensity.sp[i,sp] ~ dnorm(mu.gam.intensity[i],
                                       tau.gam.intensity[i])
   }
 }


## ******************************************************
## Species phi & gam in each region
## ******************************************************

## Set the effect of each region for each species.
## Parameterization sets region 1 as the intercept:
## all other regions are contrasts off of region 1.

mu.phi.region[1]<-0
mu.gam.region[1]<-0
sigma.phi.region[1]<-0
sigma.gam.region[1]<-0

for(sp in 1:nsp){
  phi.reg.sp[1,sp] <- 0
  gam.reg.sp[1,sp] <- 0
}


for(reg in 2:4) {
  mu.phi.region[reg] ~ dnorm(0, 0.001)
  mu.gam.region[reg] ~ dnorm(0, 0.001)
  sigma.phi.region[reg] ~ dunif(0,20)
  sigma.gam.region[reg] ~ dunif(0,20)
  tau.phi.region[reg] <- 1/(sigma.phi.region[reg]*sigma.phi.region[reg])
  tau.gam.region[reg] <- 1/(sigma.gam.region[reg]*sigma.gam.region[reg])

  for(sp in 1:nsp){
    phi.reg.sp[reg,sp] ~ dnorm(mu.phi.region[reg], tau.phi.region[reg])
    gam.reg.sp[reg,sp] ~ dnorm(mu.gam.region[reg], tau.gam.region[reg])
```

```
  }
}

## Set priors for the effects of all traits in each land-use

for(i in 1:3) {
  phi.trait[i]  ~ dnorm(0,0.001)
  gam.trait[i]  ~ dnorm(0,0.001)
  phi.trait2[i]  ~ dnorm(0,0.001)
  gam.trait2[i]  ~ dnorm(0,0.001)
  phi.trait3[i]  ~ dnorm(0,0.001)
  gam.trait3[i]  ~ dnorm(0,0.001)
  phi.trait4[i]  ~ dnorm(0,0.001)
  gam.trait4[i]  ~ dnorm(0,0.001)
}

## *******************************************************
## Establish core likelihood function
## *******************************************************

## Species-specific detectability.
## A function of land-use intensity,
## and additional species, site, and year random effects .

for(sp in 1:nsp) {
  p.0[sp] ~ dnorm(0, tau.p.0)
  for (yr in 1:nyear) {
    for(site in 1:nsite){
      p.site.yr.sp[site,yr,sp] ~ dnorm(0, tau.p.site.yr.sp)

      logit(p[site,yr,sp]) <- p.0[sp] +
                p.intensity[intensity[site]] +
                  p.year[yr] +
                    p.site[site] +
                      p.site.yr.sp[site,yr,sp]
    } #\site
  } #\yr
} #\sp

## Occupancy for species in a site, over all years

for(sp in 1:nsp) {
  for(site in 1:nsite) {

    ## occupancy in year 1, equilibrium expectation
    ## gamma / (1 - phi + gamma)

    mu.psi.1[site,1,sp] <- gam[site,sp]/ (1-phi[site,sp]+gam[site,sp])
    psi[site,1,sp] <- mu.psi.1[site,1,sp] *
      region.presence[sp,region[site]]
    Z[site,1,sp] ~ dbern(psi[site,1,sp])

    ## detectability in year 1
```

```
     E[site,1,sp] <- Z[site,1,sp]*p[site,1,sp]

     # Assess model fit using Chi-squared discrepancy
     # Compute fit statistic 'eval' for observed data
     eval[site,1,sp] <- pow(sum(X[site,1,,sp]) -
                                 (E[site,1,sp]*nrep[site,yr+1,sp])),2) /
                                   ((E[site,1,sp]*nrep[site,yr+1,sp]) + 0.5)
     # Generate replicate data and compute fit stats for them
     eval.new[site,1,sp] <- pow(sum(X.new[site,1,,sp]) -
                                 (E[site,1,sp]*nrep[site,yr+1,sp]),2) /
                                   ((E[site,1,sp]*nrep[site,yr+1,sp]) + 0.5)

#L75
     for(rep in 1:nrep[site,1,sp]) {
       X[site,1,rep,sp] ~ dbern(E[site,1,sp])
       X.new[site,1,rep,sp] ~ dbern(E[site,1,sp])
     }

    ## Effect of region, species and trait values
    ## on persistence and colonization probabilities
    ## in subsequent years.

     logit(phi[site,sp]) <-
       phi.reg.sp[region[site],sp] +
         phi.intensity.sp[intensity[site],sp] +
           phi.trait[intensity[site]] * trait[sp] +
             phi.trait2[intensity[site]] * trait2[sp] +
               phi.trait3[intensity[site]] * trait3[sp] +
                 phi.trait4[intensity[site]] * trait4[sp] +
                   phi.site[site]

     logit(gam[site,sp]) <-
       gam.reg.sp[region[site],sp] +
         gam.intensity.sp[intensity[site],sp] +
           gam.trait[intensity[site]] * trait[sp] +
             gam.trait2[intensity[site]] * trait2[sp] +
               gam.trait3[intensity[site]] * trait3[sp] +
                 gam.trait4[intensity[site]] * trait4[sp] +
                    gam.site[site]


     for(yr in 1:(nyear-1)) {

       psi[site,yr+1,sp] <-
         (Z[site,yr,sp] * phi[site,sp] +
          (1-Z[site,yr,sp]) * gam[site,sp]) *
            region.presence[sp,region[site]]

       Z[site,yr+1,sp] ~ dbern(psi[site,yr+1,sp])

       E[site,yr+1,sp] <- Z[site,yr+1,sp]*p[site,yr+1,sp]

     # Assess model fit using Chi-squared discrepancy
```

```
       # Compute fit statistic 'eval' for observed data
       eval[site,yr+1,sp] <- pow(sum(X[site,yr+1,,sp]) -
                                    (E[site,yr+1,sp]*nrep[site,yr+1,sp]),2) /
                                      ((E[site,yr+1,sp]*nrep[site,yr+1,sp]) +
0.5)
       # Generate replicate data and compute fit stats for them
       eval.new[site,yr+1,sp] <- pow(sum(X.new[site,yr+1,,sp]) -
                                    (E[site,yr+1,sp]*nrep[site,yr+1,sp]),2) /
                                      ((E[site,yr+1,sp]*nrep[site,yr+1,sp]) +
0.5)

         for(rep in 1:nrep[site,yr+1,sp]) {
           X[site,yr+1,rep,sp] ~ dbern(E[site,yr+1,sp])
           X.new[site,yr+1,rep,sp] ~ dbern(E[site,yr+1,sp])

         } # \rep
       } # \yr
     } # \site
   } # \sp
  fit <- sum(eval[,,])
  fit.new <- sum(eval.new[,,])

 } # \model.jags
```

Appendix 2: Simple Occupancy model for habitat shift

```
model.jags<-function() {

    ## *******************************************************
    ## Detection Priors
    ## *******************************************************

    # Priors for random effects
    sigma.p.0 ~ dunif(0,10)
    tau.p.0 <- 1/(sigma.p.0*sigma.p.0)

    sigma.p.site ~ dunif(0,10)
    tau.p.site <- 1/(sigma.p.site*sigma.p.site)

    sigma.p.site.year.sp ~ dunif(0,10)
    tau.p.site.year.sp <- 1/(sigma.p.site.year.sp*sigma.p.site.year.sp)


   ## Fixed effect of land-use intensity

    for(i in 1:3) {
      mu.p.intensity.pre[i] ~ dunif(0,1)
      mu.p.intensity[i] <- logit(mu.p.intensity.pre[i])
    }

    ## Species, Site, and Year random effects

    for (site in 1:nsite){
      p.site[site]~dnorm(0, tau.p.site)
    }

    for (yr in 1:nyear){
      p.year[yr]~dnorm(0, tau.p.year)
    }

    for(sp in 1:nsp) {
        p.0[sp] ~ dnorm(0, tau.p.0)

        for (site in 1:nsite){
          for (yr in 1:nyear){

            p.site.year.sp[site,yr,sp]~dnorm(0, tau.p.site.year.sp)

            ## Overall detection probability
            logit(p[site, yr, sp]) <- p.0[sp] +
                                       mu.p.intensity[intensity[site]] +
                                          p.site[site] +
                                            p.year[yr] +
                                              p.site.year.sp[site,yr,sp]

        }
      }
    }
```

```
## *******************************************************
## Occupancy effects - Land use intercept, and rainfall slope
## *******************************************************

for(i in 1:3) {
  ## Land-use intercept
  mu.psi.int.pre[i] ~ dunif(0, 1)
  mu.psi.intensity[i] <- logit(mu.psi.int.pre[i])
  sigma.psi.intensity[i] ~ dunif(0,10)
  tau.psi.intensity[i]<-1/(sigma.psi.intensity[i] * sigma.psi.intensity[i])
  ## Rainfall slope for each land-use
  mu.psi.int.rf[i] ~ dnorm(0, 0.001)
  sigma.psi.int.rf[i] ~ dunif(0,10)
  tau.psi.int.rf[i]<-1/(sigma.psi.int.rf[i] * sigma.psi.int.rf[i])

  for(sp in 1:nsp){
    psi.intensity[i,sp] ~ dnorm(mu.psi.intensity[i],
                                     tau.psi.intensity[i])

    psi.int.rf[i,sp] ~ dnorm(mu.psi.int.rf[i],
                                     tau.psi.int.rf[i])
    }
  }


## *******************************************************
## Occupancy random effects
## *******************************************************

sigma.psi.site ~ dunif(0,10)
tau.psi.site <- 1/(sigma.psi.site*sigma.psi.site)

for (sp in 1:nsp){
  for (site in 1:nsite){
    psi.site[site,sp]~dnorm(0, tau.psi.site)
  }
}


## *******************************************************
## Establish core likelihood function
## *******************************************************

for(sp in 1:nsp) {
  for(site in 1:nsite) {
    for(yr in 1:nyear) {

    logit(psi[site,yr,sp]) <-
              psi.intensity[intensity[site], sp] +
               psi.int.rf[intensity[site], sp]*rainfall[region[site]] +
                psi.site[site,sp]

      Z[site,yr,sp] ~ dbern(psi[site,yr,sp])
```

```
        E[site,yr,sp] <- Z[site,yr,sp]*p[site,yr,sp]

        # Assess model fit using Chi-squared discrepancy
        # Compute fit statistic 'eval' for observed data
        eval[site,yr,sp] <- pow(sum(X[site,yr,,sp]) -
                                  (E[site,yr,sp]*nrep[site,yr,sp]),2) /
                                    ((E[site,yr,sp]*nrep[site,yr,sp]) + 0.5)
        # Generate replicate data and compute fit stats for them
        eval.new[site,yr,sp] <- pow(sum(X.new[site,yr,,sp]) -
                                    (E[site,yr,sp]*nrep[site,yr,sp]),2) /
                                     ((E[site,yr,sp]*nrep[site,yr,sp]) + 0.5)


        for(rep in 1:nrep[site,yr,sp]) {
          X[site,yr,rep,sp] ~ dbern(E[site,yr,sp])
          X.new[site,yr,rep,sp] ~ dbern(E[site,yr,sp])
        }
      }
    }
  }
 fit <- sum(eval[,,])
 fit.new <- sum(eval.new[,,])
}
```

Appendix 3: Simple Occupancy model for habitat affiliation

```
model.jags<-function() {

    ## ******************************************************
    ## Detection Priors
    ## ******************************************************

    # Priors for species, site, and year random effects
    sigma.p.0 ~ dunif(0,10)
    tau.p.0 <- 1/(sigma.p.0*sigma.p.0)

    sigma.p.year ~ dunif(0,10)
    tau.p.year <- 1/(sigma.p.year*sigma.p.year)

    sigma.p.site ~ dunif(0,10)
    tau.p.site <- 1/(sigma.p.site*sigma.p.site)

    sigma.p.site.year.sp ~ dunif(0,10)
    tau.p.site.year.sp <- 1/(sigma.p.site.year.sp*sigma.p.site.year.sp)

    ## Fixed effect of land-use intensity
    for(i in 1:3) {
      mu.p.intensity.prior[i] ~ dunif(0,1)
      mu.p.intensity[i] <- logit(mu.p.intensity.prior[i])
    }

    ## Species, Site, and Year random effects

    for (site in 1:nsite){
      p.site[site]~dnorm(0, tau.p.site)
    }

    for (yr in 1:nyear){
      p.year[yr]~dnorm(0, tau.p.year)
    }


    for(sp in 1:nsp) {
        p.0[sp] ~ dnorm(0, tau.p.0)

        for (site in 1:nsite){
          for (yr in 1:nyear){

            p.site.year.sp[site,yr,sp]~dnorm(0, tau.p.site.year.sp)

            ## Overall detection probability
            logit(p[site, yr, sp]) <- p.0[sp] +
                                           mu.p.intensity[intensity[site]] +
                                            p.year[yr] +
                                              p.site[site] +
                                                p.year[yr] +
```

```
                                             p.site.year.sp[site,yr,sp]
       }
     }
   }
   ## ******************************************************
   ## Occupancy priors - Land use component
   ## ******************************************************


## Fixed effect of intensity. Contrast with forest.
   mu.psi.intensity[1]<-0 # Set forest to zero
   sigma.psi.intensity[1]<-0

   for(i in 2:3) {
     mu.psi.intensity[i] ~ dnorm(0,0.01)
     sigma.psi.intensity[i] ~ dunif(0,20)
     tau.psi.intensity[i]<-1/(sigma.psi.intensity[i] * sigma.psi.intensity[i])
   }

## Random effect of species in each intensity
## (allows species specific habitat affiliations)
for(sp in 1:nsp){
    psi.intensity.sp[1,sp] <- 0 # All species affiliation with
                                # forest set to zero.
    for (i in 2:3) {
         psi.intensity.sp[i,sp] ~ dnorm(mu.psi.intensity[i],
                                        tau.psi.intensity[i])
    }
}


   ## ******************************************************
   ## Occupancy priors - Region component
   ## ******************************************************

   # Fixed effect of region. Mean value for each region
   for (reg in 1:4){
    mu.psi.reg[reg]~dnorm(0, 0.01)
       sigma.psi.region[reg] ~ dunif(0,20)
       tau.psi.region[reg] <- 1/(sigma.psi.region[reg]*sigma.psi.region[reg])

     for (sp in 1:nsp){
       psi.reg.sp[reg,sp] ~ dnorm(mu.psi.reg[reg], tau.psi.region[reg])
         # Interpreted as each species occupancy in forest in each region
     }
   }


   ## ******************************************************
   ## Occupancy priors - Random site effect
   ## ******************************************************
   sigma.psi.site ~ dunif(0,10)
   tau.psi.site <- 1/(sigma.psi.site*sigma.psi.site)
```

```
  for (sp in 1:nsp){
    for (site in 1:nsite){
      psi.site[site,sp]~dnorm(0, tau.psi.site)
    }
  }

  ## ******************************************************
  ## Establish core likelihood function
  ## ******************************************************

  for(sp in 1:nsp) {
    for(site in 1:nsite) {
      for(yr in 1:nyear) {

 logit(psi[site,yr,sp]) <-
                psi.intensity.sp[intensity[site], sp] +
                   psi.reg.sp[region[site],sp] +
                      psi.site[site,sp]


        Z[site,yr,sp] ~ dbern(psi[site,yr,sp])

        E[site,yr,sp] <- Z[site,yr,sp]*p[site,yr,sp]

        # Assess model fit using Chi-squared discrepancy
        # Compute fit statistic 'eval' for observed data
        eval[site,yr,sp] <- pow(sum(X[site,yr,,sp]) -
                                  (E[site,yr,sp]*nrep[site,yr,sp]),2) /
                                    ((E[site,yr,sp]*nrep[site,yr,sp]) + 0.5)
        # Generate replicate data and compute fit stats for them
        eval.new[site,yr,sp] <- pow(sum(X.new[site,yr,,sp]) -
                                    (E[site,yr,sp]*nrep[site,yr,sp]),2) /
                                     ((E[site,yr,sp]*nrep[site,yr,sp]) + 0.5)


        for(rep in 1:nrep[site,yr,sp]) {
          X[site,yr,rep,sp] ~ dbern(E[site,yr,sp])
          X.new[site,yr,rep,sp] ~ dbern(E[site,yr,sp])
        } #/rep
      } #/year
    } #/site
  } #/sp
fit <- sum(eval[,,])
fit.new <- sum(eval.new[,,])
} #/model
```