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Diversity Regulation in Local Communities: Colonization and Extinction Dynamics in North American Birds

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ABSTRACT

Aim: Species richness of local communities may be regulated via negative diversity dependence of colonization or positive diversity dependence of extinction rate. We explore whether and how bird communities are regulated and what determines extinction and colonization rates across communities.

Location: North America, spanning the United States and Canada.

Time Period: 1995–2019.

Major Taxa Studied: Passerines.

Methods: We used long-term community time-series from the North American Breeding Bird Survey (BBS) to analyse spatial patterns in colonization and extinction rates across 646 survey routes. We linked these rates to community species richness, proportion of species pool represented in the local community, richness relative to resource level, mean population size and stability and environmental productivity and its seasonality (approximated by Normalized Difference Vegetation Index, NDVI). We used correlation analyses, generalized linear models, Random Forest and Structural Equation Modelling (SEM).

Results: Extinction and colonization rates are highly balanced across sites, supporting the idea of diversity regulation. Both rates are lower at sites with higher equilibrium species richness and especially at sites with a higher proportion of the species pool represented in the local community, supporting the diversity-dependence of colonization rate. In contrast, we did not find any evidence for local diversity-dependence of extinction rate. However, extinction rates increase with decreasing population sizes of species and are negatively affected by environmental productivity that influences population stability.

Main Conclusions: Local bird community richness appears regulated, but this regulation stems primarily from a progressive exhaustion of the number of potential colonists from a species pool as local species richness increases, not from a decreasing population size with increasing richness. Local bird diversity is then determined by the interaction of the size of the species pool with local population persistence modulated by environmental productivity. Diversity dynamics is thus essentially equilibrial, but regional and local diversity appear regulated by different mechanisms.

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1 | Introduction

The dynamics of biodiversity across spatial and temporal scales is a central topic in ecology (Mittelbach et al. 2007; Ricklefs 2007; Storch et al. 2022). A long-standing debate concerns whether the dynamics is unbounded (i.e., diversity can potentially increase without limits) or regulated (i.e., diversity fluctuates around an equilibrium value; Cornell 2013; Harmon and Harrison 2015; Rabosky and Hurlbert 2015). Recently, growing evidence has accumulated that diversity is regulated at multiple spatial and temporal scales (Storch and Okie 2019). Analyses of the fossil record show that although diversity increased rapidly during some periods (specifically following mass extinctions and key innovations such as the colonization of land), there is no evidence for uncontrolled exponential growth over any extended interval of the Phanerozoic (Alroy 2010; Close et al. 2017, 2020; Rineau et al. 2022). Contemporary geographic diversity patterns likewise suggest the existence of region-specific limits to diversity and thus its regulation—different evolutionary histories have led to remarkably congruent diversity gradients (Hawkins et al. 2012). At local scales, temporal variation of species richness also often appears to be bounded by community-level regulation (Brown et al. 2001; Parody et al. 2001; Gonzalez and Loreau 2009; Gotelli et al. 2017; Magurran et al. 2018).

A general mechanism of diversity regulation was verbally outlined already by Darwin (1859): 'The amount of life [...] supported on an area must have a limit, depending so largely as it does on physical conditions; therefore, if an area be inhabited by very many species, each or nearly each species will be represented by few individuals; and such species will be liable to extermination from accidental fluctuations in the nature of the seasons or in the number of their enemies'. Since then, various approaches have been proposed to formalize diversity regulation (MacArthur and Wilson 1963; Walker and Valentine 1984; Hubbell 2001; Rabosky 2013; Okie and Storch 2025). The key property of the regulated diversity dynamics shared by all models is negative diversity dependence, analogous to negative density dependence in the dynamics of populations: species richness regulation may emerge if at least one of the fundamental rates determining species richness of an area (speciation, colonization, extinction) is diversity dependent.

That said, there are several pathways in which diversity regulation can be achieved (Box 1). At large spatial (regional) scales where colonization rates are negligible, both speciation and extinction probability can be diversity dependent via the dependency of the rates on population size (Storch and Okie 2019; Okie and Storch 2025). In line with Darwin's quote above, as the number of species increases, their population sizes must decrease if the total amount of resources remains approximately constant, which eventually leads to increasing extinction probability (Storch et al. 2018) and which can decrease speciation probability if speciation is also population size-dependent (Rabosky 2013; Okie and Storch 2025). At more local scales where colonization dominates over speciation, colonization rate may decrease with increasing number of species within a community due to a different mechanism, namely a progressive exhaustion of the number of potential colonists from the species pool. This is the dominant regulation factor in the Theory of Island Biogeography (TIB; MacArthur and Wilson 1963, 1967), as the simplest version of the TIB assumes that total extinction rate is just proportional to the number of species on the island (Rosenzweig 1995), that is, per-species extinction rate is diversity independent (Box 1). However, MacArthur and Wilson (1963, 1967) admit that per-species extinction rate may be also diversity dependent due to increasing competition and consequently decreasing population sizes with increasing species richness (which is reflected by the convex shape of the extinction curve).

It is not clear which processes drive species richness regulation within local mainland communities in which speciation rate is unimportant and colonization rate is, at least in comparison to islands, rather high. Species richness within these communities is ultimately driven by the balance between colonization and extinction, and in principle both these processes may be diversity dependent due to similar reasons as assumed by the TIB. Additionally, both colonization and extinction may be responsible for the differences in equilibrium species richness between different sites. There are thus multiple possibilities how colonization rates may interact with extinction rates in driving local species richness, and these possibilities can be classified based on whether respective rates are diversity dependent or independent, and whether the diversity-independent components of the rates (i.e., the propensities of the rates) vary across the sites (Figure 1). Our aim here is to determine which scenario of local species richness regulation is most plausible, using the most comprehensive data on spatiotemporal community dynamics, namely the North American Breeding Bird Survey (BBS; Ziolkowski Jr. et al. 2022) that encompasses bird communities across large part of North America sampled for several decades.

Unlike other empirical studies addressing local-scale diversity regulation (Brown et al. 2001; Gotelli et al. 2017) that examined temporal fluctuations within individual communities, we focus on spatial patterns in species extinction and colonization. To distinguish different regulation scenarios depicted in Figure 1, we formulate a set of hypotheses focused on distinct aspects of potential diversity regulation. First, it is necessary to evaluate if bird communities are regulated. Hypothesis 1 (H1; Table 1) thus posits that local extinctions and colonizations are balanced, that is, higher rates of extinctions are associated with higher colonization rates. The next two alternative hypotheses comprise the ways through which the regulation operates. Hypothesis 2 (H2) states that species richness regulation is driven mostly by diversity-dependent extinction rates (columns C and D in Figure 1), while Hypothesis 3 (H3) states that diversity-dependent colonization rate is the predominant regulation factor (rows 3 and 4 in Figure 1).

Although H2 and H3 cannot be tested directly, there are indicative patterns that may serve as evidence for one or another. First, the direction of the relationship between equilibrium species richness and both rates across sites (indicated by the +, −, or 0 symbols associated with each scenario in Figure 1) is informative in this regard. It is evident from Figure 1 that a positive relationship between equilibrium species richness and both rates occurs only if extinction rate is positively diversity dependent, that is, if H2 holds (scenarios denoted by + sign appear only in columns C and D). Similarly, a negative relationship between equilibrium species richness and the rates occurs only if colonization rate is negatively diversity dependent, that is, if H3 holds (scenarios denoted by − sign appear only in rows 3 and 4). Note, however, that the implications are unidirectional—if one of the rates is diversity dependent, it by itself does not imply any particular relationship between the

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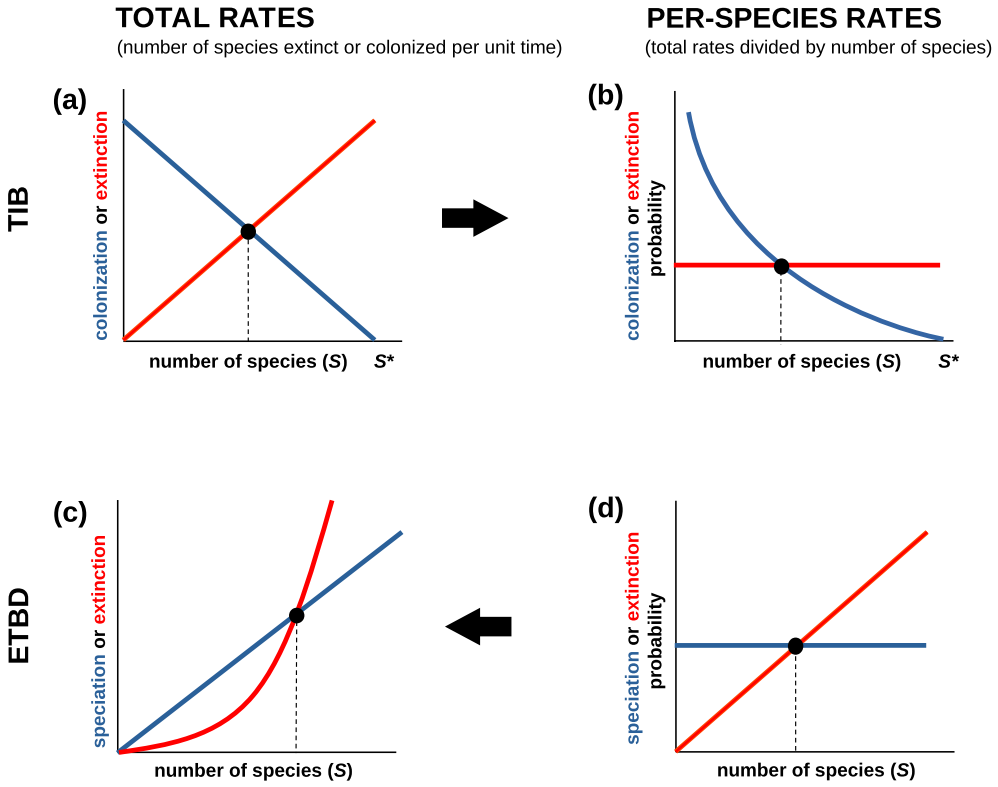
BOX 1 | Species richness regulation formalized by the simplest versions of two contrasting theories, namely the Theory of Island Biogeography (TIB, top) and the Equilibrium Theory of Biodiversity Dynamics (ETBD, bottom).

The TIB is based on total rates of extinction and colonization (panel a). While extinction rate increases (in this simplest version; Rosenzweig 1995) with species richness just for statistical reasons (more species means that more of them can go extinct), colonization rate declines with richness due to a progressive exhaustion of species pool – the more species are on the island, the less species remain available for colonization, which is defined as an arrival of new species. Total extinction rate E is thus a linear function of the number of species S, $E = aS$, where a is the slope equal to extinction probability of one species. Total colonization rate C is a declining linear function of S, $C = m(S^* - S)$, where m is the mean colonization probability and S^* is the size of the species pool. If we express both the rates in a per-species way, plotting extinction and colonization probabilities instead of total rates (panel b), per-species rate of extinction is constant (equal to a), while per-species colonization rate turns into $\frac{C}{S} = \frac{mS^*}{S} - m$ (represented by hyperbola, since m and S^* are constants).

In contrast to the TIB, ETBD is a theory focused on biodiversity dynamics at large regions where colonization is negligible (Okie and Storch 2025) and thus it formalizes biodiversity dynamics using per-species rates of speciation and extinction (panel d). In its simplest version (Storch et al. 2018), the per-species speciation rate is constant, while the per-species extinction rate increases with species richness due to decreasing mean population sizes of species competing for shared resources (with a function that depends on the shape of the population size dependence of extinction probability, here for simplicity depicted as a straight line). When plotted using total rates (panel c), the speciation rate increases linearly with species richness (for the same reason why the extinction rate increases linearly within the TIB), while the extinction rate increases as an upward-accelerating function of S. All equilibria (black dots at the intersections of respective curves) are stable, as a movement left towards lower species richness leads to lower extinction than colonization (speciation) rates and vice versa.



rates and equilibrium species richness, and if there is no such relationship, it does not imply anything about diversity dependencies, as the absence of correlation may stem from different combinations of rates and their diversity dependencies (Figure 1).

Additional evidence in favour of H2 can be obtained by relating extinction rates to species richness relative to resource levels. If extinction rate does not positively correlate with equilibrium species richness across sites, it still can be diversity dependent, yet this dependency can be masked by different amounts of resources and consequently total community abundance across sites. In the strict formulation of the more-individuals hypothesis (MIH; Storch et al. 2018), species richness is proportional to community abundance, and mean population size thus remains constant, leading to constant extinction rate—but this proportionality is maintained via rising extinction rates when species richness temporally rises above the level in which mean population abundance is in equilibrium. H2 thus implies that extinction probabilities should be higher at sites where species richness is higher than what would be expected based on available resources

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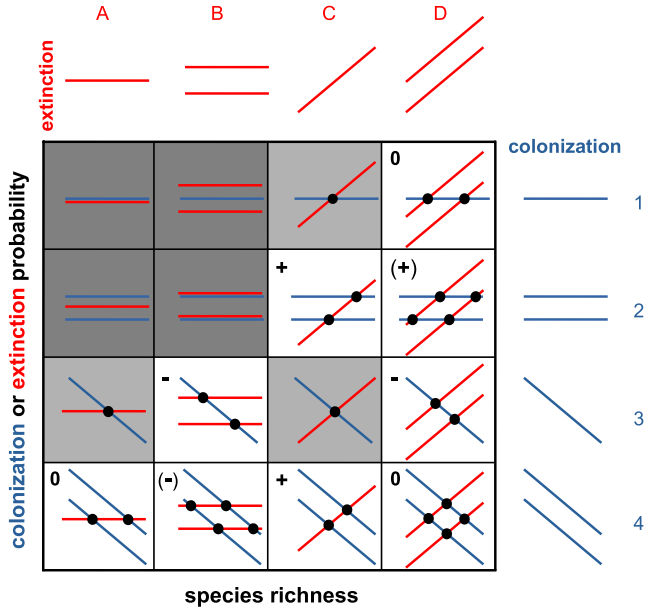

FIGURE 1 | Alternative scenarios of local-scale diversity regulation arising from different configurations of extinction (red) and colonization (blue) rates (defined as per-species probabilities). The scenarios are classified based on (i) whether colonization and extinction rates are diversity dependent (rows 3 and 4; columns C and D, respectively) and (ii) whether rate propensities (i.e., the positions of the lines) vary across sites (rows 2 and 4; columns B and D, respectively). Rate propensities represent the species richness-independent components of the rates, which may be site-specific and influenced by environmental factors. For example, sites experiencing higher seasonality may exhibit a higher propensity for extinction, that is, higher realized extinction rate than sites with the same species richness but lower seasonality. Sixteen scenarios can be then distinguished: Four of them (dark grey) are irrelevant as there is no equilibrium if none of the rates is diversity dependent; three additional scenarios (light grey) would lead to just one equilibrium richness and thus are also not relevant in a system in which we observe different species richness equilibria. Note also that we ignore the possibilities that extinction rates are negatively and colonization rates positively diversity dependent, as these do not have any biologically founded rationale and would not lead to regulation (i.e., stable equilibria). For each site, equilibrium species richness and the realized extinction and colonization rates occur at the intersection of corresponding lines and are denoted by a black circle. Different scenarios then yield different directions of the relationship between equilibrium species richness and realized extinction/colonization rates across sites, as indicated by the symbols (+, −, 0) associated with each scenario (symbols in parentheses indicate relatively weaker relationships than those without parentheses). By examining the relationship between species richness and extinction/colonization rates across sites using empirical data from many local communities, we can infer nature of diversity-dependence of the rates (here, for simplicity, the scenarios are represented by only two or four different equilibria). It is evident that positive relationship between equilibrium species richness and both rates across sites (scenarios denoted by +) appears only in the cases when extinction rate is positively diversity dependent (columns C and D), while negative relationship between richness and the rates (scenarios denoted by −) appears only in the case of diversity dependence of colonization rate (rows 3 and 4). Note that if we observe no relationship between species richness and the rates (scenarios denoted by 0), we cannot unequivocally distinguish whether colonization or extinction rate (or both) are diversity dependent.

TABLE 1 | List of the hypotheses and associated predictions tested in the study. H1–H4 correspond to Hypotheses 1–4 in the text.

Hypothesis	Prediction/Indicative pattern[a]
H1: *Local species richness is regulated.*	*Local extinction and colonization probabilities are highly correlated across sites.*
H2: *Species richness regulation is driven mostly by diversity dependence of extinction rates.*	**H2a**: *Positive relationship between equilibrium species richness and extinction/colonization probabilities across sites (rationale in* Figure 1*).*
	H2b: *Extinction probability is higher at sites where species richness is higher than what would be expected based on NDVI.*
H3: *Species richness regulation is driven mostly by diversity dependence of colonization rates.*	**H3a**: *Negative relationship between equilibrium species richness and extinction/colonization probabilities across sites (rationale in* Figure 1*)*
	H3b: *Negative relationship between colonization probability and proportion of species pool represented in the local community.*
H4: *Differences in extinction rates drive variation in species richness among sites.*	**H4a**: *Extinction probability negatively depends on population sizes.*
	H4b: *Extinction probability is affected by the properties of the environment that drive population size-independent characteristics of population dynamics, namely population stability.*

[a]H2a and H3a are not predictions (i.e., necessary consequences of a hypothesis), as their implications are only unidirectional. The positive relationship between equilibrium species richness and extinction/colonization probabilities across sites (H2a) supports the hypothesis of diversity dependence of extinction rate (H2) (Figure 1, scenarios denoted by + symbol). However, diversity dependence of extinction rates (H2) does not by itself imply any particular relationship between the extinction/colonization probabilities and equilibrium species richness (Figure 1, columns C and D). The analogous reasoning applies to H3a.

(NDVI; H2b). H3, in contrast, implies that colonization and extinction probabilities are higher if local species richness is low relative to the size of the species pool, since diversity dependence of colonization rate is assumed to be driven by progressive exhaustion of the pool of potential colonists as local richness approaches regional richness. In other words, if colonization rate is diversity dependent, it should be negatively related to the ratio between local and regional richness (H3b).

H2 and H3 address the question which rate is responsible for diversity regulation. A distinct question is which rate drives the differences in equilibrium species richness among sites and what determines this rate. It is reasonable to expect that richness differences are driven by differences in extinction rates (Hypothesis 4; H4), as there are several external factors that could potentially affect extinction propensities, independently of their potential diversity dependence. Two additional predictions thus comprise extinction rates. H4a states that extinction probability negatively depends on population sizes, regardless of whether they are

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linked to the diversity dependence (i.e., decreasing population sizes with increasing diversity) or to different population sizes in different environments. H4b postulates that extinction probability is additionally affected by the properties of the environment that drive population size-independent characteristics of population dynamics, namely population stability.

2 | Methods

2.1 | Data

To evaluate patterns in local extinctions and colonizations, we used data from the North American Breeding Bird Survey (BBS; Ziolkowski Jr. et al. 2022; https://www.pwrc.usgs.gov/bbs/), the most comprehensive community time-series survey worldwide. The BBS is an annual, volunteer-based standardized bird count conducted across the United States and Canada during the peak of the breeding season, encompassing more than 4000 survey routes. Each route (our basic data point) is approximately 40 km long and includes 50 stops spaced about 800 m apart. At each stop, an observer performs a 3-min point count, recording every bird individual heard or seen within an approximately 400 m radius. We excluded all records that did not meet the official BBS quality criteria—such as those collected during fog, heavy precipitation, or high winds—or that deviated from the standard BBS sampling protocol. Following previous studies (Boucher-Lalonde et al. 2014; Rich and Currie 2018), we restricted our analysis to passerines (315 species), as songbirds have a higher probability of detection using the BBS methodology than non-passerines.

The number of routes surveyed has grown rapidly since the inception of BBS, while not every route was surveyed every year and many have been abandoned. To resolve the trade-off between time span and number of routes, we restricted our analysis to the period 1995–2019 (there was no survey in 2020) and selected the routes with at least 20 pairs of consecutively surveyed years within this period. To reduce spatial bias stemming from uneven route density, we performed spatial subsampling based on Bird Conservation Regions (BCRs), following Jarzyna and Jetz (2017). In regions with more than 30 routes, we iteratively excluded routes with the shortest distances to neighbouring routes until each BCR contained at most 30 routes. This temporal and spatial filtering resulted in 646 routes analysed (Figure 2).

To estimate resource availability for each BBS route, we used normalized difference vegetation index (NDVI) from NASA's LP DAAC for 2000–2019. The dataset used (MOD13A3; Didan 2021; https://lpdaac.usgs.gov/products/mod13a3v061/) provides monthly NDVI values at a 1 km spatial resolution. For each route, we extracted NDVI values using a 1 km buffer and averaged the monthly data to obtain annual NDVI. While some studies preferred summer NDVI over annual NDVI, assuming that the summer estimate better predicts bird diversity (Hurlbert 2004; Dobson et al. 2015), we chose to use annual NDVI because our focus was on local extinctions, which we expect to be influenced not only by productivity during the breeding season (at least for resident species). We also examined the correlation between mean extinction probability per route and both NDVI measures, finding a slightly stronger correlation with annual NDVI.

We additionally calculated seasonality as the difference between June NDVI (the peak of vegetation season) and the lowest monthly NDVI observed during the winter months (November to March). We also considered alternative measures of seasonality, such as the relative difference between June and minimum winter NDVI (i.e., the difference divided by June NDVI) or the coefficient of variation of monthly NDVI values. However, these measures suffer from the problem of a correlation with the annual NDVI. In contrast, the simple difference between June and minimum winter NDVI showed no correlation with annual NDVI and thus provides an independent measure of the seasonality of a route (Toszogyova and Storch 2019).

2.2 | Variables

We characterized every BBS route in every year t by several variables. We defined an interannual per-species *extinction probability* as a number of species present in year t but absent in year $t+1$ divided by the total number of species present in year t. Similarly, we defined *colonization probability* as the number of species present in year t but absent in year $t-1$ divided by the number of species present in year t.

We are aware that this definition of extinction also includes false extinctions (apparent absences of species recorded in the previous year due to observation error) and this likely leads to overestimation of true local extinctions. Several previous studies have used multispecies occupancy models to account for species imperfect

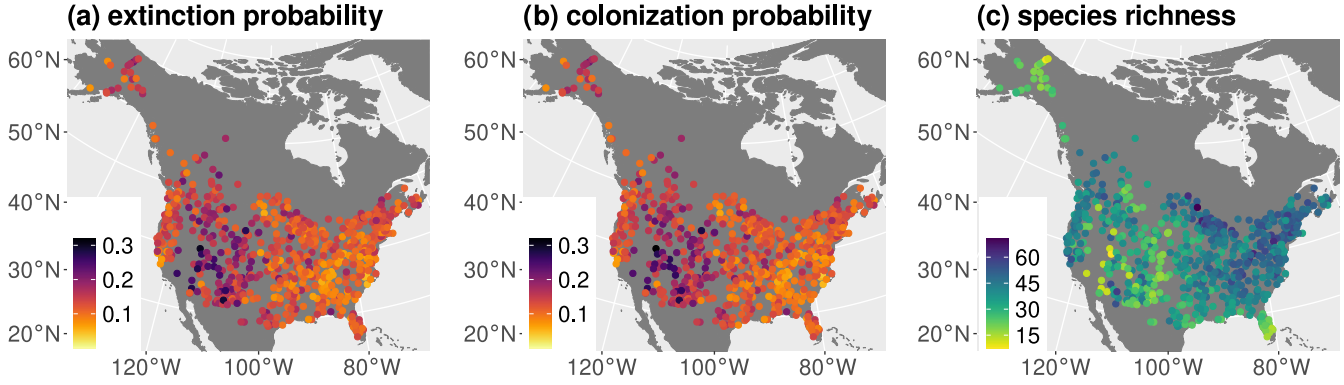

FIGURE 2 | The 646 BBS routes used in the analysis and their (a) mean extinction probability, (b) mean colonization probability and (c) mean species richness.

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detection in BBS data (Jarzyna and Jetz 2017, 2018). However, because our study also considers species abundances and not only occurrences, this approach was not applicable. We therefore primarily calculated extinctions and colonizations using raw data. Although this approach may introduce some bias in the extinction and colonization estimates, it is likely to be small, as species with low detection probabilities are rarely recorded as present and are thus seldom falsely classified as extinct (Boucher-Lalonde et al. 2014). Nevertheless, we additionally assessed the potential impact of false extinctions and colonizations, using several approaches. First, we repeated all analyses after excluding singletons (species with a population of one individual) from the calculation of extinction and colonization probabilities, since the disappearance and reappearance of singletons may often result from observation error. Specifically, if a species absent in year $t+1$ had a population size of one individual in year t, we did not count this absence as extinction (and analogously for colonization). Second, we recalculated extinctions and colonizations using 3-years time bins and performed all analyses using this merged-years approach. Third, we performed all the analyses after removing species that can be classified as transients. The idea that some species are only transients (and their occurrence is thus likely driven by accidental dispersal from nearby suitable habitat and does not represent true extinction and colonization events) stems from the observation that temporal occupancy distribution is bimodal (Snell Taylor et al. 2018) – core species occur in most sampling periods and likely maintain viable populations at the site, and transient species are detected only occasionally in the time series. We thus classified species at each site as core or transient following the method of Coyle et al. (2013) and repeated all analyses using only core species. Detailed methods for defining core and transient species and for the 3-years bins analysis are provided in the Supporting Information.

We further characterized bird community of every route in every year t by several variables. We calculated species richness (S_t) and total number of individuals (J_t). We determined mean population size using two approaches. First, we used the simple arithmetic mean of population sizes of individual species, $\frac{1}{S_t}\sum N_{i,t}$, where $N_{i,t}$ is the abundance of ith species in year t, or $\frac{J_t}{S_t}$. However, given the typically unbalanced, right-skewed species abundance distributions (SADs), arithmetic mean may not accurately reflect typical population sizes, being strongly dependent on extremes (namely the few most abundant species). We thus also calculated arithmetic mean of log-transformed population sizes of individual species, $\frac{1}{S_t}\sum log(N_{i,t})$, that is, the logarithm of the geometric mean of population sizes. Even though community SADs are typically right-skewed and roughly log-normal, making geometric mean an appropriate measure of typical population sizes, the communities somehow differ in the exact shape of their SADs. Therefore, we also calculated following measures of dominance and rarity: relative dominance (abundance of the most abundant species divided by J_t), proportion of singletons (number of singleton species divided by S_t) and proportion of rare species (number of rare species divided by S_t, where a rare species is defined as a species having population smaller than 5% of J_t).

We also calculated temporal variability in population sizes (hereafter *population variability*). To do that, we first calculated population growth rate for every species i and year t as $r_{i,t} = log\frac{N_{i,t}}{N_{i,t-1}}$ (i.e., it is only defined for species with non-zero abundances in both years). Then, we averaged absolute values of these population growth rates across species to get the mean value of population variability for a route in year t, $r_t = \frac{1}{S_t}\sum|r_{i,t}|$.

Finally, we calculated the mean value of each variable described above for every BBS route as the arithmetic mean of year-specific values.

To determine whether a route had more or fewer species than expected given its resource supply, we modelled the relationship between species richness and NDVI as a power law. Specifically, we fit a linear ordinary least squares (OLS) regression of log-transformed species richness (mean across years for each route) on log-transformed NDVI. We then extracted the residuals from this regression, so that positive residuals indicate higher-than-expected species richness and negative residuals indicate lower-than-expected richness for a given level of productivity. We refer to these values as the *residuals of S ~ NDVI*.

We also approximated the species pool for each route using two approaches. First, we counted the number of species recorded across all analysed BBS routes within each BCR—defined as ecologically distinct regions with broadly similar bird communities—and assigned this BCR-level species pool to every route in that region. Second, we counted all species observed on a given route together with those on its four nearest neighbouring routes, if the route had at least four neighbouring routes within a 200-km radius (a condition not met for 62 of the 646 routes). The two metrics were correlated and yielded similar results, so we report only the analyses using the BCR-based species pool.

2.3 | Statistical Analyses

We used several complementary statistical approaches. First, we examined simple bivariate relationships between the variables. We created correlation matrix of all variables using R package 'corrplot' (Wei and Simko 2024) and Spearman's rank correlation coefficient.

Second, we fitted several generalized linear models (GLMs) with a quasibinomial distribution and a logit link function to model extinction and colonization probabilities. We chose this approach because the response (extinction or colonization probability) is bounded between 0 and 1 but does not follow a binomial distribution, as both total and extinct/colonized species counts are non-integer values, representing means across years. We modelled the probabilities as functions of (i) species richness (H2a and H3a), (ii) the proportion of species pool represented in the local community (i.e., the ratio of local to regional species richness; H3b) and (iii) the joint effects of species richness and NDVI (to test H2b, which states that extinction should be higher at sites where species richness exceeds the levels expected from resource availability). In the multiple regression, predictors were standardized (by subtracting their mean and dividing by their standard deviation) to allow direct comparison of regression coefficients.

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Third, to directly compare the relative importance of individual variables in predicting extinction probability, we performed variable importance analysis using the Random Forest algorithm (Breiman 2001). Random Forest is a machine learning algorithm to construct decision trees and its advantage is that it can fit nonlinear relationships and interactions between parameters, without a need to specify them a priori (Hastie et al. 2009). We used the *randomForest* function from the R package 'randomForest' (Liaw and Wiener 2002). Unlike the default setting of the function, we constructed 50,000 trees for each response variable (extinction probability and extinction probability after excluding singletons). We then used the decrease in out-of-bag mean squared error (MSE) as a measure of the importance of the variables. This measure is considered to be a more robust measure than the commonly used decrease in node impurity (Loecher 2022). For each tree in the random forest, MSE was calculated using the out-of-bag data. This process was repeated after permuting the values of each predictor variable. The differences in MSE before and after permutation were averaged across all trees and standardised by dividing by the standard deviation of these differences.

Finally, to evaluate direct and indirect effects of population sizes, population variability and NDVI on extinction probability (H4b), we formulated a series of structural equation models (SEMs). Because R packages that allow the use of GLMs within SEMs (like 'piecewiseSEM'; Lefcheck 2016) do not support the quasibinomial distribution, we implemented SEMs using the standard 'lavaan' package (Rosseel 2012) with linear models. All variables were standardized prior to analysis to facilitate model estimation, and extinction probability and population variability were log-transformed to meet normality assumptions of SEMs. We also included species richness in the models, because it is linked to extinction probability as well as to NDVI (Figures 4, 5). Although we assumed no direct effect of NDVI on extinction, we initially specified a full model including all possible (reasonable) paths. That is, extinction probability was predicted by the direct effects of population sizes, population variability, species richness and NDVI and by indirect effects of NDVI mediated through the other three variables. We then removed a non-significant path (namely the path from NDVI to population sizes) and present this reduced model, as it had lower AIC than the full model.

3 | Results

3.1 | Geographic Trends and Balance of Extinction and Colonization (H1)

Extinction and colonization probabilities reveal a pronounced longitudinal trend, low extinction/colonization probabilities characterizing the eastern part of North America, while the western part shows higher extinction/colonization probabilities (Figure 2). Species richness at individual BBS routes fluctuated throughout the study period (1995–2019), but these fluctuations appear bounded, without clear directional trends over time (Figure 3a). In accord with the assumption of diversity regulation, colonization and extinction probabilities are well balanced (H1; Figure 3; Figure 2a,b) – across BBS routes, extinction and colonization probabilities are highly correlated ($r = 0.98$; Figure 3b), and this pattern persists after removing singletons ($r = 0.96$; Figure 3b). Excluding singletons lowers the estimated extinction probability (because many real and apparent extinctions involve singletons), but the estimates remain strongly correlated with those based on the raw data ($r = 0.94$; Figure 3c). The close balance between extinction and colonization probabilities is also evident when only core species are considered ($r = 0.96$; Figure 3d), while the probabilities are less well balanced when using 3-year bins, although extinctions and colonizations are still symmetrically distributed around the 1:1 axis ($r = 0.76$; Figure 3d) (for possible reasons, see Supporting Information).

3.2 | Drivers of Diversity Regulation: Diversity Dependence of Extinction and Colonization Rates (H2, H3)

Extinction and colonization probabilities are negatively correlated with species richness across BBS routes, such that species-rich communities exhibit lower per-species probabilities of both extinction and colonization (i.e., lower temporal turnover; Figure 4a; $r = -0.55$ for extinction, $r = -0.57$ for colonization). Predictions of quasibinomial GLMs with a logit link are shown in Figure 4a. Extinction probability declines significantly with increasing species richness ($F_{1,644} = 281.32$, $p < 0.001$, explained deviance = 0.31), and the same pattern is observed for colonization probability ($F_{1,644} = 320.65$, $p < 0.001$, explained deviance = 0.33). This observation is in line with H3, which states that species richness regulation is driven primarily by diversity dependence of colonization rates (Figure 1, rows 3 and 4, scenarios associated with minus sign). This is further supported by the finding that both rates are negatively correlated with the proportion of species pool represented in the local community (H3b, Figure 4b; $r = -0.68$ for extinction, $r = -0.70$ for colonization). Predictions of quasibinomial GLMs with a logit link are shown in Figure 4b. Colonization probability declines significantly with the proportion of species pool ($F_{1,644} = 646.91$, $p < 0.001$, explained deviance = 0.50), and the same pattern is observed for extinction probability ($F_{1,644} = 599.17$, $p < 0.001$, explained deviance = 0.48).

In contrast, we did not find evidence for the role of extinction rate in the diversity regulation (H2). Although H2, which states that diversity is regulated by positive diversity dependence of extinction rate, cannot be unequivocally rejected based on the observation that extinction probability is negatively correlated with species richness (as it is still compatible with scenario 3D in Figure 1, which assumes diversity dependence of both rates), there is no additional indication supporting this dependence. Extinction probability is not higher in communities whose richness is higher than expected based on resources (NDVI) (H2b), that is, in communities with higher residuals of S ~ NDVI (Figure 4c). Visual inspection of Figure 4c shows that high extinction probabilities (dark points) are associated with low NDVI and low species richness per se, rather than with the position relative to the modelled S ~ NDVI relationship (i.e., rather than with high positive residuals of this relationship as predicted by H2b). Formally, when species richness and NDVI are included jointly in the model predicting extinction probability (quasibinomial GLM with a logit link and standardized predictors), both variables show significant and comparably strong partial negative effects on extinction probability (species richness: $\beta = -0.129$, $F_{1,636} = 321.33$, $p < 0.001$; NDVI: $\beta = -0.131$, $F_{1,635} = 101.02$, $p < 0.001$; explained deviance = 0.40). The significant negative

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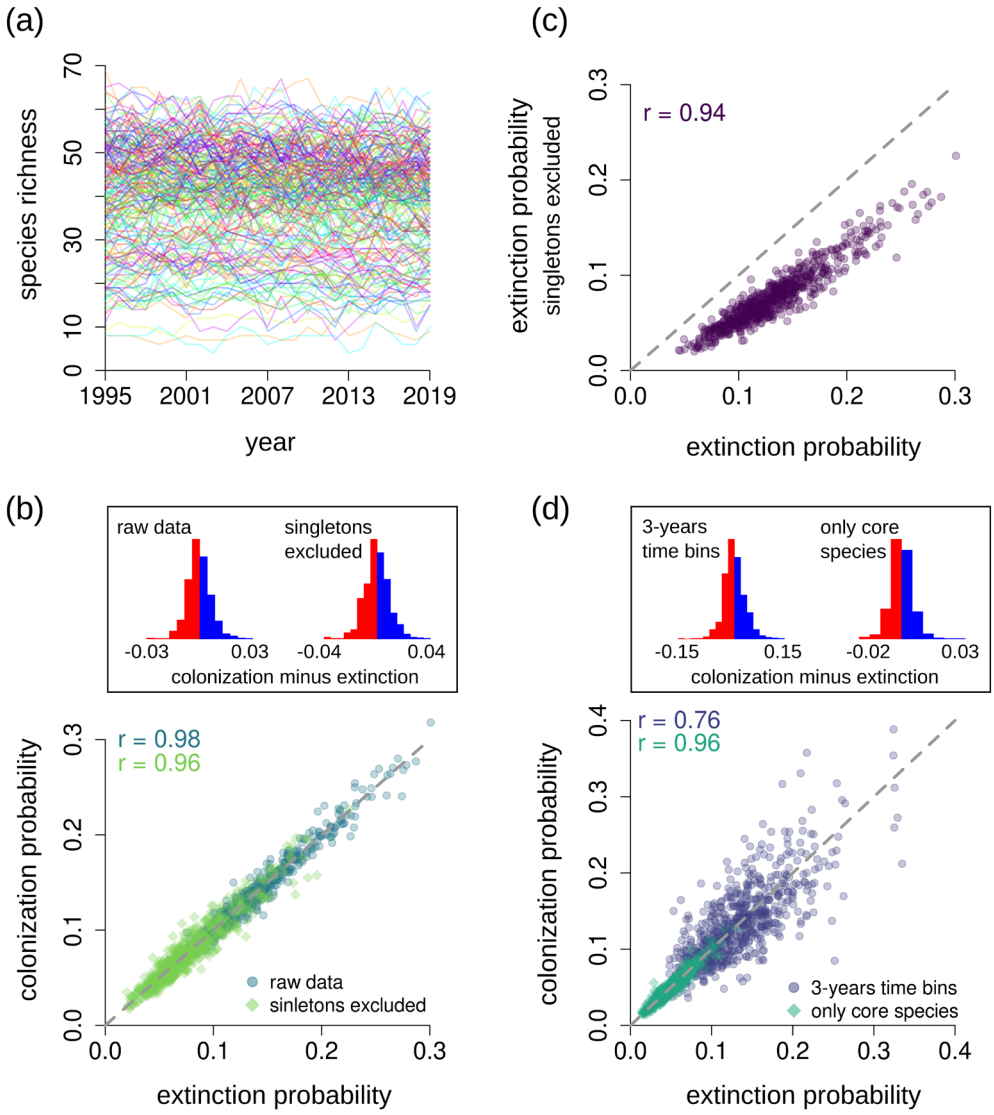

FIGURE 3 | Balance of colonizations and extinctions (H1). (a) The fluctuation of species richness on each BBS route over the study period (only the routes with all years surveyed are shown). (b, d) Local extinction and colonization probabilities are highly balanced. This holds when extinction probabilities are calculated from raw data (b, turquoise circles), as well as when singletons are excluded (specifically, the extinction of a singleton is not counted as an extinction and analogously for colonization) (b, lime green diamonds). Extinction probability calculated after excluding singletons is lower but remains highly correlated with extinction probability calculated using raw data (c). When the rates are calculated using 3-years time bins (instead of year-to-year extinctions and colonizations), extinction and colonization probabilities are not so perfectly balanced, but they are still systematically distributed around 1:1 axis (d, blue circles). When only core species are considered within each community (BBS route), extinction and colonization rates are again highly balanced (d, green diamonds). The histograms above panels b and d show the distributions of the differences between colonization and extinction probabilities. Although comparison of the rates for all species (b, circles) and for core species only (d, diamonds) shows that high proportion of extinctions and colonizations involve transient species (as the rates are lower when only core species are considered), some extinction and colonization dynamics remain even among core species (the rates for all species and for core species only are also correlated—Figure S9).

partial effect of species richness means that extinction probability decreases with increasing species richness for the same level of NDVI. This is the opposite than expected by H2b. Altogether, the patterns observed are compatible with scenarios 3B and 3D (and possibly 4B), but there is no clue that would provide a higher support for any of them, as there is no evidence for the diversity-dependence of extinction.

We obtained similar results also in the analyses that used 3-years bins and in those restricted to core species (Supporting Information, Figure S1–S14). The observed relationships are almost identical when using 3-years bins (Figure S3) and somewhat weaker—but still significant and of the same direction—when only core species are considered (Figure S11 and corresponding results in the Supporting Information).

3.3 | Predictors of Extinction Probabilities (H4)

On the other hand, the link between population size and extinction probability, which is a necessary component of the potential mechanism of diversity-dependence of extinction rates, has been supported (H4a). Communities with lower average population sizes exhibit higher extinction probabilities (Figure 5).

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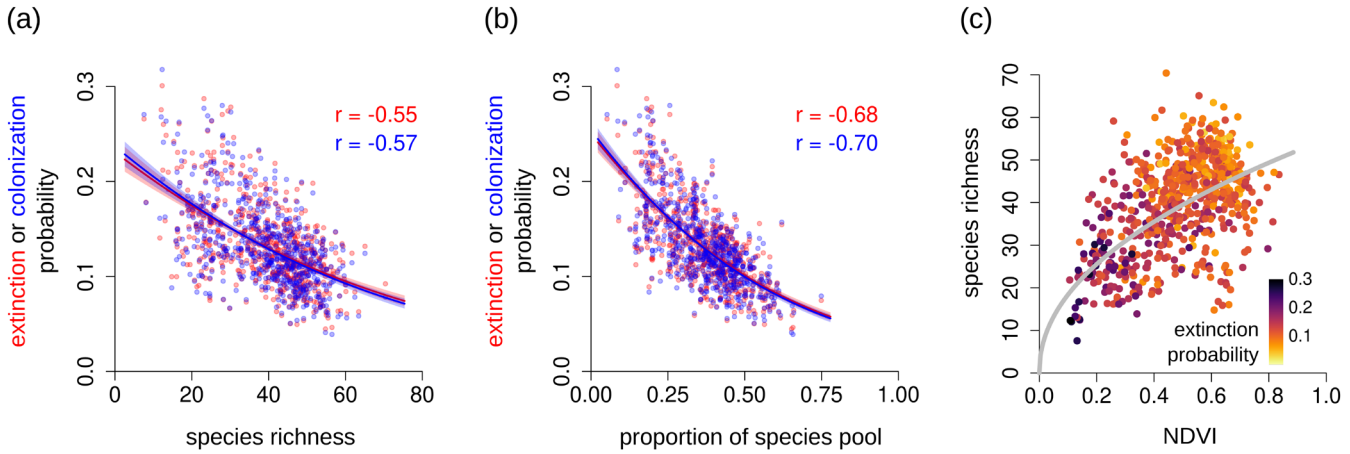

FIGURE 4 | Links between species richness and rates of colonization and extinction. (a) Extinction (red) and colonization (blue) probabilities decrease with species richness across sites, in line with H3a. (b) Extinction and colonization probabilities further decrease with the proportion of species pool represented in the local community, in line with H3b. Both these pieces of evidence support the idea of diversity-dependence of colonization rates and the consequent major role of colonization rate in diversity regulation (H3). Correlation coefficients and the prediction of GLM together with 95% confidence intervals are shown in a-b. (c) Extinction probability in relation to NDVI and species richness of a community. The prediction of the model log(S) ~ log(NDVI) is shown in grey. According to H2b, extinction probability should be higher at sites where species richness exceeds the level expected based on NDVI, that is, at sites with high (positive) residuals of the depicted model. This prediction is not supported: High extinction probabilities (dark points) are associated with low NDVI and low species richness per se, rather than with the position relative to the modelled relationship.

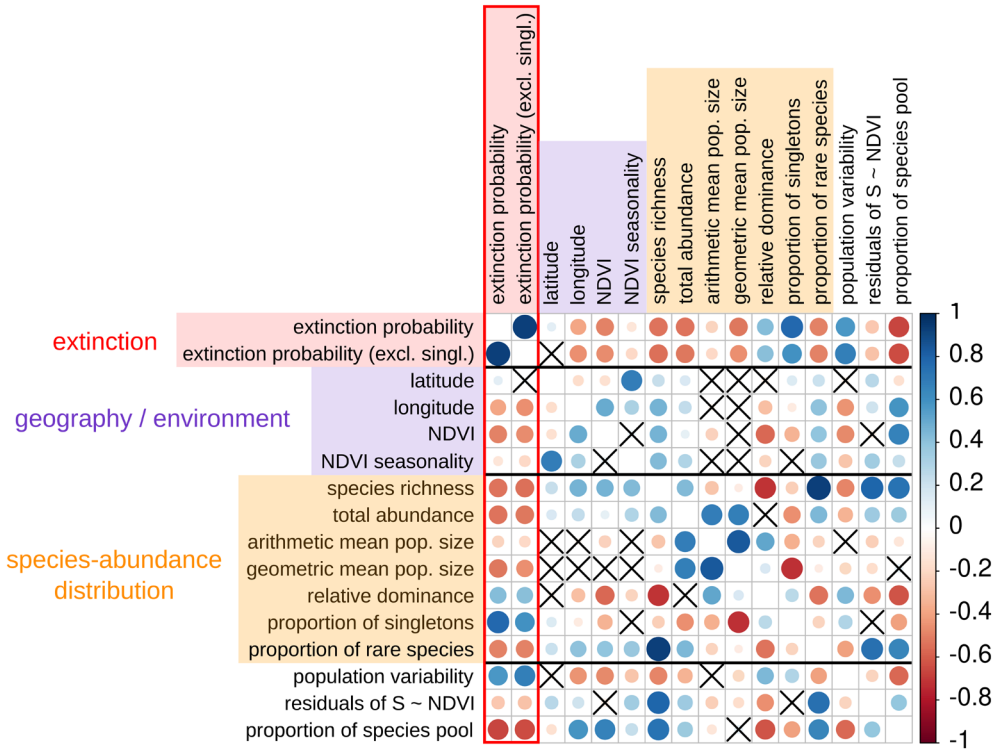

FIGURE 5 | Correlation matrix showing the relationships between evaluated variables. Correlations with extinction probability are presented in the first two columns (highlighted by the red rectangle) or rows. The colour and size of the circles represent Spearman's correlation coefficient, as indicated by the scale bar (ranging from strong positive correlations in dark blue to strong negative correlations in dark red). Also, larger circles denote a stronger correlation. Crosses denote non-significant (at $\alpha = 0.01$) correlations. The variables are colour-coded into 3 main categories for better visibility. *Excl. singl.* denotes the extinction probability after excluding singletons (specifically, not counting the extinction of a singleton as an extinction).

Notably, the geometric mean of population size is a considerably better predictor of extinction probability ($r_s = -0.51$) than the arithmetic mean ($r_s = -0.20$), likely due to the sensitivity of the arithmetic mean to extreme (high) abundances and complementary lower sensitivity to abundances of most species. We thus use the geometric mean of population sizes in subsequent analyses.

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Importantly, the proportion of singletons is an even stronger predictor of extinction probability ($r_s = 0.77$), and, consistent with H4b, there is also a strong effect of population variability ($r_s = 0.58$) – sites with more variable populations have higher extinction probability. Population variability is not strongly correlated with population sizes—it shows a nonsignificant correlation with the arithmetic mean ($r_s = -0.03$) and only a weak correlation with the geometric mean of population sizes ($r_s = -0.20$; Figure 5), so that population size and population variability represent independent determinants of extinction probability. The strengths of these bivariate correlations between extinction probability and the other variables are very similar for the 3-year bins analysis (Figure S4), while they are generally lower in the core species analysis (Figure S12) – nevertheless, the proportion of singletons, population variability and geometric mean of population size remain the strongest correlates of extinction probability.

When comparing all the potential drivers of extinction probability simultaneously using Random Forest (Figure 6, top row), the proportion of singletons appears as the most important factor, followed by population variability, in accord with the univariate correlations in Figure 5. When singletons are excluded, population variability becomes the most important predictor, with the geometric mean of population size showing only slightly lower importance (Figure 6b). The rankings of the remaining variables vary between the different model settings (panels in Figure 6, top row). NDVI shows moderate importance, whereas NDVI seasonality has virtually no effect. This aligns with the geographical patterns of extinction probability (Figure 2), as NDVI exhibits longitudinal trend across North America, whereas NDVI seasonality follows mostly latitudinal gradient. It is also consistent with the bivariate correlations in Figure 5, where NDVI shows a relatively strong negative relationship with extinction probability, whereas seasonality exhibits only very weak correlation. The Random Forest results based on 3-year bins differ in the lower importance of population variability (Figure S5), while those based only on core species remain similar (Figure S13; for further discussion see Supporting Information). Altogether, these results support H4b stating that the properties of environment (represented interestingly by annual mean NDVI rather than NDVI seasonality) affect extinction probability via affecting population stability.

This interpretation is further supported by the SEM models (Figure 6c,d): population sizes, their variability and NDVI all (together with species richness) significantly affect extinction probability, regardless of whether singletons are included or not. However, contrary to our expectation (H4b), NDVI affects extinction probability not only indirectly—through its effect on population variability, with more productive environments supporting more stable populations—but also directly, suggesting an influence of environmental productivity on extinction that is not fully explained by population variability or population size.

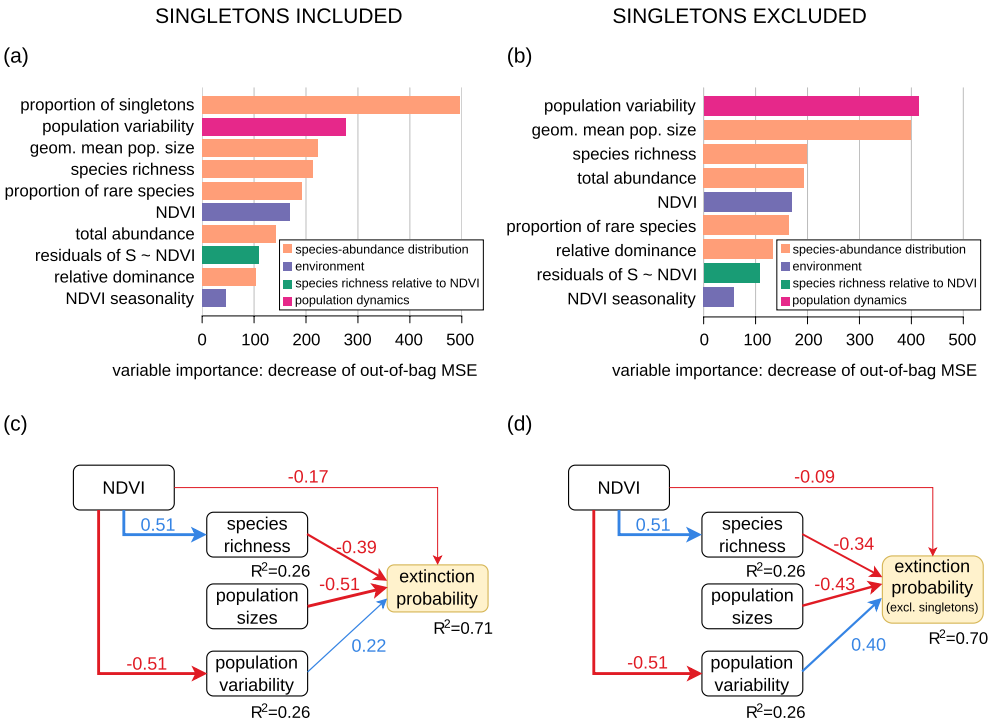

FIGURE 6 | Factors affecting extinction probability (left column) and extinction probability after excluding singletons (right column) revealed by the Random Forest analysis (top row) and structural equation models (SEMs; bottom row). Top row: Importance of evaluated variables (mean population size and additional metrics characterizing SAD of a community, population variability, residuals of S ~ NDVI and environmental variables) measured as the decrease in out-of-bag mean squared error (MSE). Variables are sorted from the most to the least important. Bottom row: SEMs showing the effects of mean population sizes (represented by geometric mean of population sizes), population variability, NDVI and species richness. Blue and red arrows represent positive and negative standardized path coefficients, respectively. Arrow thickness is scaled proportionally to the respective path coefficient. The path from NDVI to mean population sizes (i.e., the indirect effect of NDVI on species richness mediated by mean population sizes) was tested but found to be insignificant at $\alpha = 0.01$, and models that included this path have higher AIC values than the depicted ones. The direct effect of NDVI on extinction rates (i.e., not mediated by the other variables) seems to be justified, as the standardized paths coefficients are significant and models omitting this path have higher AIC values than the depicted ones.

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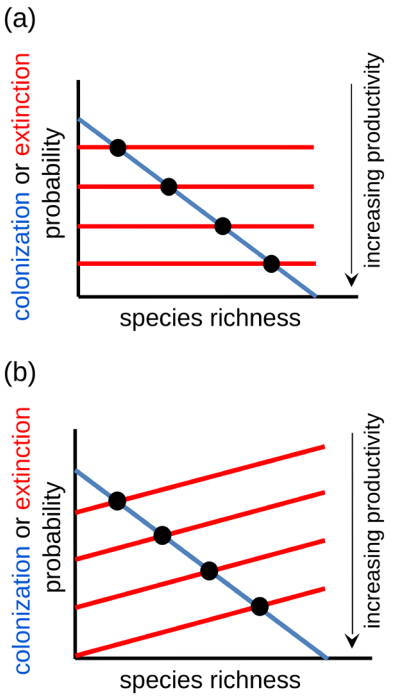

FIGURE 7 | Supported scenarios of species richness regulation. Spatial patterns of extinction and colonization probabilities across BBS routes are most compatible with the idea that the major regulation factor is negative diversity-dependence of colonization rate (blue), while differences in equilibrium species richness are driven by different levels of extinction rates (red) mediated by the environment—namely by ecosystem productivity (NDVI) affecting population stability. We did not find any direct evidence of diversity-dependence of extinction rate (a); however, it cannot be unequivocally rejected based on the observed patterns (b).

However, this effect is very weak when singletons are excluded, indicating that NDVI directly (negatively) affects mostly the number of singletons (Figure 5), and it is also missing when only core species are considered (Figure S14). Note that population sizes are not correlated with NDVI, and NDVI thus cannot affect extinction probability via the effect on population size. The results of the SEMs are similar for the 3-year bins and the core species analyses (Figures S6 and S14), with comparable values of the path coefficients (except for the insignificant direct effect of NDVI on extinction for core species), even though these models explain less variation in extinction probability (R^2 between approximately 0.40–0.50; Figures S6 and S14).

In summary, although observed patterns cannot unequivocally confirm or reject diversity-dependence of extinction rates (and thus distinguish scenarios 3B and 3D in Figure 1), they are most compatible with the idea that diversity-dependence of colonization rate is the major regulation factor, while differences in species richness are driven by different levels of extinction rates mediated by the environment—namely ecosystem productivity estimated using annual NDVI (Figure 7).

4 | Discussion

The balance between colonization and extinction rates across communities that widely differ in species richness indicates that local bird species richness is regulated (H1). This does not necessarily exclude the possibility that there are slight long-term changes of species richness. Jarzyna and Jetz (2017) used much longer time series of BBS (1969–2013) and reported an average increase in species richness until approximately 2000, followed by a period of non-significant change and then a slight decline after 2007. Our shorter study period (1995–2019) spans all three periods they identified (increase, stability and decline) and extends the analysis until 2019. Therefore, directional changes in species richness might have occurred across the routes in some periods. However, these changes were probably too small (Jarzyna and Jetz 2017 reported average annual change of +0.75%) and not directional during the whole study period to be detected using the interannual comparison of extinction and colonization rates. Notably, the idea of species richness regulation does not rely on an assumption of no change at all, but on the negative feedback between the variable in focus (in our case species richness) and its growth rate. If some rates participating in the overall growth rate (namely extinction and colonization) vary temporally, it can lead to a change of the variable even if the rates are diversity-dependent.

The observed negative correlation between species richness and per-species rates of both colonization and extinction appears most compatible with the scenarios in which local species richness is regulated by the negative diversity dependence of colonization rate (Figure 1), presumably due to the progressive exhaustion of the species pool as species richness increases. This is supported by the strong correlation between the rates and the proportion of the species pool represented in the local community. Interestingly, this correlation was even stronger than the correlation between the rates and local richness itself, further supporting the idea of diversity-dependence of colonization rate as the main regulating factor (H3). Although there are notorious issues with the definition of species pool that always comprises some circularity (Cornell and Harrison 2014), these issues could potentially bias the relationship towards a weaker correlation, as a circular establishment of species pool would lead to species pool size which would be closer to species richness of local communities. We thus can, with rather high confidence, attribute diversity regulation to the almost trivial relationship between colonization probability and the relative number of potential colonists (assuming relatively temporarily constant species pool). This is also the main mechanism of diversity regulation postulated by the TIB (MacArthur and Wilson 1963, 1967; Box 1).

These findings do not imply that extinction rate plays no role. It certainly affects species richness variation among local communities—since local bird species richness does not simply mirror species pool (in such case there would be no variation in the proportion of species pool represented in the local community), local species richness variation must be driven by different propensity to either colonization or extinction (i.e., different position of respective lines in Figure 1). But different propensity of colonization should not lead to a negative relationship between species richness and respective rates unless the extinction propensities also differ (Figure 1, scenario 4B). It is thus most probable that spatial diversity variation is driven mostly by spatial variation in local extinction rates (see Figure 1 columns B and D; H4). On the other hand, we do not provide any direct evidence of diversity dependence of extinction rate. Extinction rates do not

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increase with species richness (H2a), nor with species richness controlled for the resource level (H2b; Figure 4c), and although the geometric mean of population sizes affects extinction probability, it does not seem to be related to species richness, nor to any other variable (Figure 5). Therefore, there is no indication of decreasing population size with increasing richness. The problem is, however, that the absence of evidence is not evidence of absence. If higher species richness is associated with lower rates of colonization (and extinction) due to the colonization diversity-dependence depicted above, there is no reason why higher species richness controlled for the resource level should be (in equilibrium) associated with higher rates even if extinction was diversity-dependent (Figure 1, scenario D3)—this test could be informative only under the scenarios in which species richness was not generally negatively associated with the rates.

If spatial variation of extinction rate drives local species richness variation (H4), it is natural to ask which properties of bird communities affect extinction rates. Both simple correlations and random forests revealed the effects of population size and associated measures like total community abundance, proportion of rare species, or the proportion of singletons (although the effect of the latter measure can be spurious, which was the reason we repeated all analyses with singletons excluded). This is not surprising, as the role of population size in extinction probability is well-established knowledge (Pimm et al. 1988; Rosenzweig 1995; Ovaskainen and Meerson 2010). Interestingly, however, population variability appeared equally important, or even slightly more important than population size (namely when singletons were excluded). Moreover, NDVI revealed a strong (negative) effect on population variability and thus appears as the factor that drives diversity variation via its positive effect on population stability. Note that because colonization and extinction rates are tightly correlated, our statistical models cannot distinguish whether population size, population variability and NDVI primarily affect extinction or colonization. Our interpretation that these factors act through extinction is based on ecological reasoning—namely that smaller and more variable populations are more extinction-prone—rather than on the statistical structure of the models alone. Our results thus indicate that higher environmental productivity elevates species richness via allowing populations to persist longer in the environment, and higher richness then leads to decreasing colonization rates due to the exhaustion of species pool, so that resulting richness stabilizes at the value where the lowered extinctions are balanced by respective colonization rates.

Although these conclusions represent a relatively straightforward interpretation of the observed patterns, there are some caveats. Most importantly, our measures of extinction and colonization may be affected by imperfect detection. Certainly, some detected extinction and colonization events are not actual disappearances and reappearances of species but are driven by undetected presences of species in some years. Although these effects are more important at individual observation points and less at the level of a whole transect, it has been necessary to avoid them as much as possible. We achieved it with three approaches which complemented our main analyses, namely by excluding singletons whose presence and absence are most affected by detectability effects, by using longer time windows (3 years instead of 1 year) and by limiting our analyses to the core species, according to Coyle et al. (2013). Across all these robustness checks, correlations between extinction probability and the key predictors were of the same sign and similar magnitude as those observed in the main analyses, with the core-species analysis showing somewhat attenuated but still significant relationships. There is thus no reason to expect that the detectability issue generates a pronounced bias.

Our findings that environmentally driven local extinction rates drive the differences in local bird community richness, while diversity-dependent colonization rate acts as the regulating factor, shed light on the nature of bird communities and the relationship between local and regional diversity, a classical issue in community ecology (Ricklefs and Schluter 1993). On one hand, community diversity regulation via the exhaustion of the pool of potential colonists, together with the lack of evidence of diversity-dependence of local extinction rate, implies that local bird communities are open systems representing just samples from the species pool, that is, from regional richness (Caley and Schluter 1997). The dynamics of local species richness is thus analogous to diversity dynamics postulated by the Theory of Island Biogeography where colonization is the key process and species pool determines local richness, while species pool itself (i.e., regional richness) is driven by a different set of processes (Ricklefs and Schluter 1993; Caley and Schluter 1997). On the other hand, the finding that local species richness is driven by local extinction rate implies that local bird communities are by no means random samples from the species pool, as assumed by some authors (Blackburn and Gaston 2001). Their diversity is not driven just by sampling, but by the propensity of the environment to maintain stable populations which can, in the long term, also affect regional species richness, that is, the species pool. The most realistic overall picture is thus a multilevel dynamical process in which regional richness affects local richness via colonization, but local richness is linked to local population extinction, which eventually propagates up to the extinction at the regional level. Since extinction at the regional level depends on the regional population size, it can be diversity dependent at large spatial scales (but only there), in accord with the Equilibrium Theory of Biodiversity Dynamics, which focuses on these scales (Okie and Storch 2025; Storch et al. 2026).

5 | Conclusion

If local communities are regulated by diversity dependence, it can operate through negative diversity dependence of colonization or positive diversity dependence of extinction rate, or both. Spatial patterns of colonization and extinction in local bird communities across North America are compatible with the scenario in which colonization rate is diversity dependent, while varying extinction rate drives species richness variation across the communities (Figure 7). Diversity dependence of colonization rates is, in line with the Theory of Island Biogeography, a simple consequence of progressive exhaustion of the pool of potential colonists with increasing local richness and bird communities in this respect appear open, dependent on species pool and not regulated via diversity-dependent extinction rates. However, diversity dependence of extinction rates via decreasing population sizes with increasing richness cannot be entirely excluded using observed patterns, and the observed negative effect of population size on extinction probability indicates that there is a potential

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for such a mechanism. Moreover, the environment, namely its productivity measured using NDVI, seems to determine local bird species richness via affecting population variability and generally species persistence, so that local community diversity is determined by the interplay of factors affecting regional species pool and local extinction probability.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Breeding Bird Survey data are available at https://doi.org/10.5066/P97WAZE5 (Ziolkowski Jr. et al. 2022), NDVI data are available at https://lpdaac.usgs.gov/products/mod13a3v061/ (Didan 2021). Code and processed data supporting this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5dv41nshz (Bohdalková and Storch 2026).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Relationships between rates calculated using single consecutive years and those calculated using consecutive 3-years bins. **Figure S2:** The 646 BBS routes used in the supplementary analysis and their (a) mean extinction probability and (b) mean species richness, calculated using 3-years bins. **Figure S3:** Analogue to Figure 4 in the main analysis for the rates calculated using 3-years bins. (a) Extinction (red) and colonization (blue) probabilities decrease with species richness across sites, in line with hypothesis 3. (b) Extinction and colonization probabilities further decrease with the proportion of species pool represented in the local community, in line with hypothesis 3. Correlation coefficients and the prediction of GLM together with 95% confidence intervals are shown in a-b. (c) Extinction probability in relation to NDVI and species richness of a site. The prediction of model log(S) ~ log(NDVI) is shown in grey. According to hypothesis 2, extinction probability should be higher at sites where species richness exceeds the level expected based on NDVI, that is, at sites with high (positive) residuals of the depicted model. This prediction is not supported: High extinction probabilities (dark points) are associated with low NDVI and low species richness per se, rather than with the position relative to the modelled relationship. **Figure S4:** Correlation matrix showing the relationships between evaluated variables calculated as stated in the Method section of the supplementary analysis (extinction and colonization probability, species richness and residuals of S~NDVI calculated using 3-years bins). The colour and size of the circles represent Spearman's correlation coefficient, as indicated by the scale bar (ranging from strong positive correlations in dark blue to strong negative correlations in dark red). Also, larger circles denote a stronger correlation. Crosses denote non-significant (at $\alpha = 0.01$) correlations. **Figure S5:** Importance of evaluated variables in determining (a) extinction probability calculated using 3-years bins and (b) extinction probability calculated using 3-years bins, excluding the variable *proportion of singletons*. The importance is measured as the decrease in out-of- bag mean squared error (MSE). The variables are sorted from the most to the least important. **Figure S6:** Structural equation models (SEMs) showing the effects of mean population sizes, population variability, NDVI and species richness on extinction probability calculated using 3-years bins. Blue and red arrows represent positive and negative standardized path coefficients, respectively. The path from NDVI to mean population sizes (i.e., the indirect effect of NDVI on species richness mediated by mean population sizes) was tested but found to be insignificant at $\alpha = 0.05$, and models that included this path have higher AIC values than the depicted ones. The direct effect of NDVI on extinction rates (i.e., not mediated by the other variables) seems to be justified, as the standardized paths coefficients are significant and models omitting this path have higher AIC values than the depicted ones. **Figure S7:** Histogram and probability density estimate of bird species' temporal occupancy across all 646 BBS routes examined. The temporal occupancy of a species on a route is the proportion of surveyed years in which the species was recorded present. The red solid line shows the relative frequency of each temporal occupancy level. Dotted lines indicate temporal occupancy levels used to classify species as core (≥ 0.6667) or transient (< 0.3333). 57.6% of all species across all routes ($n = 39{,}131$) were classified as core species and 28.1% as transient species. **Figure S8:** Species pools based on all species and on core species only are highly correlated across the 34 Bird Conservation Regions (BCRs) ($r = 0.91$). **Figure S9:** Relationships between rates calculated using all species (original analysis in main text; x-axes) and those calculated using only core species (supplementary analysis; y-axes). (a) Extinction probability, (b) colonization probability. **Figure S10:** Geographic patterns of mean extinction probability (a) and mean species richness (b) calculated for core species only. Because site-specific mean extinction probabilities for core species are generally lower than those based on all species, the pattern is less visible when using the original colour scale (a, larger map). Therefore, we also show the same pattern using a rescaled colour scale (smaller map above). **Figure S11:** Analogue to Figure 4 in the main analysis for variables based on core species only. (a) Extinction (red) and colonization (blue) probabilities decrease with species richness across sites, in line with hypothesis 3. (b) Extinction and colonization probabilities further decrease with the proportion of species pool represented in the local community, in line with hypothesis 3. Correlation coefficients and the prediction of GLM together with 95% confidence intervals are shown in a and b. (c) Extinction probability in relation to NDVI and

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species richness of a site. The prediction of model log(S)~log(NDVI) is shown in grey. According to hypothesis 2, extinction probability should be higher at sites where species richness exceeds the level expected based on NDVI, that is, at sites with high (positive) residuals of the depicted model. This prediction is not supported: higher extinction probabilities (darker points) are associated with low NDVI and low species richness per se (although this pattern is weaker than when considering all species), rather than with the position relative to the modelled relationship. **Figure S12:** Correlation matrix showing the relationships between evaluated variables calculated using core species only. The colour and size of the circles represent Spearman's correlation coefficient, as indicated by the scale bar (ranging from strong positive correlations in dark blue to strong negative correlations in dark red). Also, larger circles denote a stronger correlation. Crosses denote non-significant correlations. **Figure S13:** Importance of evaluated variables in determining (a) extinction probability calculated using core species only and (b) extinction probability calculated using core species only after excluding singletons. The importance is measured as the decrease in out-of- bag mean squared error (MSE). The variables are sorted from the most to the least important. **Figure S14:** Structural equation models (SEMs) showing the effects of mean population sizes, population variability, NDVI and species richness on extinction probability calculated using core species only. Blue and red arrows represent positive and negative standardized path coefficients, respectively. The paths from NDVI to mean population sizes (i.e., the indirect effect of NDVI on species richness mediated by mean population sizes) and from NDVI to extinction probability were tested but found to be insignificant at $\alpha = 0.05$.

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