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A Dispersive Force Model of Caribbean Island Biogeography

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ABSTRACT

Framework-based models serve as an important tool to describe, predict and manage ecological systems. In this paper I construct one such model, a dispersive force model based on MacArthur and Wilson's (1963) theory of island biogeography, in order to assess island species richness with varying climatic patterns. Specifically, I use island–mainland distance (*d*), insular area (*A*), a climatic dispersal parameter (f), and a climatic disturbance parameter (*h*) to calculate the insular species richness ratio at equilibrium. To test this model through hurricane impact on marine islands, it was executed with data from islands of the Dutch Caribbean. Future climatic conditions were based on the UN IPCC report's 2100 predictions with a mean global temperature rise of 2°C. Although the model was implemented with conservative estimates, all the islands tested show a significant decline in species diversity in future climatic conditions. The windward islands show a ~9% to 13% decrease in insular species richness, compared to ~2% decline on the leeward islands.

INTRODUCTION

As efforts of ecosystem management become paramount, the study of macroecological patterns becomes increasingly important to recognize and better understand ecosystem composition and behavior as these ecosystems respond to climatic changes. In fact, "process-based models, using pre-existing ecological frameworks" have been observed as being "better to manage changing systems [compared to] purely statistical modeling," especially when encountering changed conditions novel to the model (Cuddington et al., 2013). Therefore, there is a rising need to rethink traditional ecological frameworks to include factors that are significant to a changing climate and its impacts on the ecosystems in question. Theories of island biogeography fabricate one such field, where traditional frameworks work well in a descriptive sense, but they lack predictive power in terms of rapid climatic changes.

Island biogeography is particularly important to adapt to today's conditions, given the prevalence of ecological islands in the world: marine islands, coral reefs, mountain ranges, and bacterial biomes associated with plant tissue are all examples of the widespread nature of ecological islands which humans are interested in studying, conserving, and managing (Peterson et al., 2008). And given the fact that islands have proven foundational for the study, formation, and improvement of ecological theory, they represent great candidates to further push theory along into an applied field (Hutchinson, 1961). Thus, I created a model which depends on traditionally accepted factors of island biogeography theory and also incorporated factors representing climatic events. In particular, I focused on the question of hurricane occurrence and species richness equilibrium on Caribbean islands. This focus is based on the legitimate concern for island ecological stability given modeled predictions of climate change, and on the gap that exists in observing island ecology as a function of discrete yet destructive climatic events, such as hurricanes (Pachauri

et al., 2015). Additionally, Caribbean islands are relatively well-sampled in the ecological sense and well-studied in the meteorological and climatic sense, and the Caribbean is increasingly recognized as an important "biodiversity hotspot" on a global scale (UNEP).

Arguably the most well-known theory of island biogeography is the one produced by MacArthur and Wilson in 1963. At its core, its success lay in its observation of the impact of island area and distance from the mainland on the species richness of the island. Specifically, area is conceptualized to provide a saturation value of species richness, based on habitat abundance and heterogeneity: the larger the island, the greater the amount of species it can theoretically hold at an equilibrium state. Distance, on the other hand, modulates the present level of the island's saturation value: the closer the island is to the mainland, the more saturated it is with different species. The area–richness relationship is based upon Preston's species–area curve, whereas the distance-richness relationship is based on the probability of colonization over physical distances (MacArthur & Wilson, 1963; Preston, 1962).

Though newer models of biogeography have been proposed and discussed over the past few decades, none have managed to supersede the MacArthur-Wilson model. In fact, most popular and novel biogeography models build upon the theoretical foundations laid by MacArthur and Wilson. Of note is the general dynamic model (GDM), proposed by Whittaker, Triantis, and Ladle in 2008, which focuses on synthesizing the MacArthur-Wilson model with evolutionary and geologic processes, in order to capture biogeographic equilibria across larger timescales. Chen, Jiao, and Tong (2011) proposed a similar model, concerned primarily with incorporating speciation. Another branch of biogeography models maintains an interest in shorter (ecologically significant but geologically insignificant) timescales, attempting to add nuance by integrating key ecological frameworks. Gravel et al. (2011), for example, incorpo-

rate trophic levels and connectance as they build on top of MacArthur and Wilson's basic framework.

With the understanding that the MacArthur-Wilson model remains foundational, and owing to the lack of established mathematical models for island biogeography that incorporate rapid climatic shifts, I began from the broad strokes they set in 1963. Adding onto the area- and distance-dependence of species richness, I deconstructed climatic events into two factors: that of dispersal and that of disturbance, with the understanding that different climatic events provide different magnitudes of dispersal and disturbance. Though speciation, glaciation, and many other factors can be implemented to better predict island biogeography patterns, given that this model is not to be used over geological timescales, these factors were not considered as significant (Rosindell & Phillimore, 2011).

Though the model presented below has the potential to be used as a stepping stone for more general models concerned with the impacts of climatic events on insular species richness, the immediate goal of this model was to predict the patterns of change in species richness equilibria across a variety of Caribbean islands. This goal was in hopes of better understanding the impact that the intensification, as well as the decrease in frequency, of hurricanes (as is expected based on climate models) will have on insular ecological health, based on the assumption that species richness and community diversity can act as proxy to broad ecological stability and health. (Bowker et al., 2008).

METHODS

Based on the MacArthur-Wilson model of island biogeography, I begin with the assumption that insular species richness is dependent upon the influx (immigration, colonization) of species from the mainland, along with the outflux (extinction) of species from the island in question (MacArthur & Wilson 1963). Colonization (λ) is based on a function of the island's distance from the mainland, as well as a function corresponding to the dispersive force that the island experiences based on climatic events. On the other hand, Extinction (μ) is based on a function of the island's area, as well as the disturbance that the island experiences based on climatic events.

$$\lambda(S) = f(\text{distance, dispersal}) \qquad \mu(S) = f(\text{area, disturbance})$$

Distance and dispersal are forces that work in tandem, influencing and modulating one another. This is based on the rationale that colonization is fundamentally an act of dispersal over a certain distance. As such, longer distance makes dispersal less likely, and lower dispersal makes colonization less likely even at a short distance. The functions of dispersal and distance are thus multiplied through an 'and-gate.' The functions of area and disturbance, however, are interpreted as independent and additive functions that are related through an 'or-gate.' Accordingly, extinction may be conceptualized as two independent fluxes operating upon the same insular species pool: the area function portrays the possibility of species extinction through resource scarcity or niche exclusion, as both mechanisms are likelier on islands of smaller area. In contrast, climatic disturbance stands as a secondary channel of species extinction, by which climatic events, through their magnitude or frequency, may disturb populations (through drastic reductions in generational survivorship, for example) to the point that they cannot recover.

Through the understanding above, the following diagram may be used as the basis of the model:
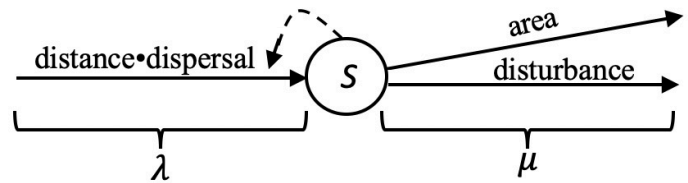
Note that S is the variable representing insular species richness as a proportion of the species on the mainland that are present on the island. In other words, $S = \frac{\text{island } \alpha-\text{diversity}}{\text{mainland } \alpha-\text{diversity}}$, with a value between (0, 1).

This model's construction implicitly assumes that the mainland species are adapted to a variety of climatic conditions, and that climatic events impacting the islands will not have a significant effect on mainland species richness, P. Additionally, no change in climatic stochasticity is assumed, and colonization from neighboring islands (internal colonization) is not considered. The dispersive and disturbance forces are also assumed to hold constant for multi-year periods, as new species richness equilibria are reached.

FUNCTION CONSTRUCTION: COLONIZATION

Colonization is inversely related to distance, as farther distances lead to increasingly slimmer chances of new species arrival from the mainland. Therefore, as the distance-based parameter (d) increases, the rate of colonization at a given value of insular species richness decreases. d is determined such as d is between (1, 10), where $d = 1$ signifies no distance (that the island is in fact part of the mainland) and $d = 10$ signifies maximum distance, beyond the scope of the data represented. This parameter is linearly correlated to distance.

The rate of colonization, as based on distance, is also linearly dependent on the species richness proportion, S, already present on the island. This implicitly accounts for the fact that as more species are present on the island, there is higher chance that an invading species might not become successfully established, based on competition and limited insular resources. The dependence of the rate of colonization on insular species richness also accounts for the fact that as more species are present on the island, it is statistically less likely that a newly invading organism will be a new species (in other words, this 'rescue effect' is implicit in the model). Mathematically, this translates to:

$$\lambda_d(S) = \frac{1}{d} - \frac{S(t)}{d}$$

The climatic event-driven dispersal onto an island, related by the parameter f, is described as a Holling type II functional response, (Holling & Buckingham, 1976), in light of the saturating effect that increases in storm magnitude or frequency lead to. An incremental increase in dispersal force, therefore, is assumed to contribute less colonization per unit of dispersal force. The summand (= 1) in the denominator was chosen to constrict most of the change attributable to f to an S-value between (0, 1).

$$\lambda_f(S) = \frac{f}{f+1}$$

f, which stands between (0, 10), is calculated for hurricanes as follows. Island hurricane and tropical storm occurrences are counted and tabulated according to the Simpson-Saffir Hurricane Wind Scale (SSHWS), for the decades between 1980 and 2020 (NOAA, 2019). Decadal frequency is calculated as the sum of all storm events for the decade, and decadal intensity is calculated as a weighted average of the decade's storm events, based on Table 1. With decadal frequency and intensity values acquired, the decade's dispersal force value, f, is calculated by multiplying the above two values. Ultimately, averaging the four decades' dispersal parameter values provides a value more representative of the island's true modern history.

SSHWS Category	Wind speed relative to Cat. 1
Tropical storm	0.28x
Category 1	1x
Category 2	1.7x
Category 3	2.3x
Category 4	3.1x
Category 5	4.5x

Table 1. *Saffir-Simpson Hurricane Wind Scale wind speed correspondence. Source: stormcarib.com (2020), NOAA (2019)*

EXTINCTION

As described by the MacArthur-Wilson model, increasing insular area allows for the island to saturate at a higher species richness. Ecologically, this relates to more abundant resources and increasingly heterogenous habitats, both leading to higher levels of coexistence and niche partitioning. Therefore, as the island area-based parameter (A) increases, the rate of extinction at a given value of insular species richness decreases.

The parameter A is calculated based on the species-area curve, as posited by Preston in 1962. Preston's observations showed a logarithmic relationship between island area and insular species richness, characterized by the relationship $S = cR^z$, where S is the insular species richness, R is the island area, and c and z are empirically-derived constants. According to this relationship, the island area-based parameter $A = \frac{cR_{island}^z}{cR_{max}^z}$.

Paralleling the relationship between colonization and distance, the rate of extinction, as based on area, is linearly dependent on S, the species richness proportion. Ecologically, this is attributable once more to competition and resource availability: higher alpha diversity on the island leads to higher levels of competition for the same resources, which leads to higher levels of extinction. Thus, the function relating the rate of extinction to area is as follows:

$$\mu_A(S) = \frac{S}{A}$$

The extinction-driving counterpart to climatic event-driven dispersal is disturbance, as large climatic event types are assumed to provide an opportunity for species dispersal as well as an opportunity for extinction through disturbance. The disturbance parameter h is described as a Holling type III function, thus proposing a sigmoid relationship between disturbance and extinction: low levels of disturbance are not expected to contribute much, if at all, to extinction. On the other hand, moderate levels of disturbance might lead to more significant rates of extinction, as the climate event would be harsh enough to lead to collapse in certain communities. There is an expected saturating effect at high levels of disturbance, as communities that are susceptible to the specific climatic event considered would collapse, but no further damage would occur to more resilient communities. Thus, the function is related as follows:

$$\mu_h(S) = \frac{h^2}{h^2 + 1} - 1$$

Like the dispersal parameter f, h is a number between (0, 10), and it is calculated as dependent on f. The ratio between f and h is to be estimated for each climatic event considered. Considering hurricanes' relatively higher level of dispersal than disturbance, $h = \frac{f}{2}$ was initially assumed.

Following original model assumptions of $\frac{dS}{dt} = (\lambda_d(S))(\lambda_f(S)) - (\mu_A(S) + \mu_h(S))$, the model is mathematically described below. Parameter and variables constraints are listed in Table 2.

$$\frac{dS}{dt} = \alpha\left(\frac{1}{d} - \frac{S(t)}{d}\right)\left(\frac{f}{f+1}\right) - \frac{\beta S(t)}{A} - \gamma\left(\frac{h^2}{h^2+1} - 1\right)$$

		Represents	Range	Notes
Parameters	d	distance from mainland	(1, 10)	((Island distance/max. distance)*9)+1 At *d*=1, the island is connected to the mainland
	A	island area	(0, 10)	Squared island size (km²)/squared maximum island size (assumed 500 km²)
	f	dispersal force	(0, 10)	Mean of decadal intensity*frequency
	h	disturbance force	(0, 10)	Derived presently from f
Variable	S	Species richness ratio	(0, 1)	Proportion of s/P

Table 2. *Summary of parameters and variables.*

The floating parameters α, β, and γ are multiplied by each of the three resulting polynomials that comprise the differential equation above, in order to best fit model predictions to actual data. Floating parameter values were calculated by transforming the equation according to the understanding that $\tilde{S} = \frac{y_0}{y_1}$, and finding values of α, β, and γ that minimized the least squares sum of the resulting equation $\sum_{i=1}^{n}(\tilde{S}_i - \sigma_i)^2 = f(\Gamma, B)$. $\tilde{S}$ represents predicted species richness at equilibrium, σ represents the actual observed species richness, Γ represents the floating parameters $\frac{\gamma}{\alpha}$, and B represents the floating parameters $\frac{\beta}{\alpha}$.
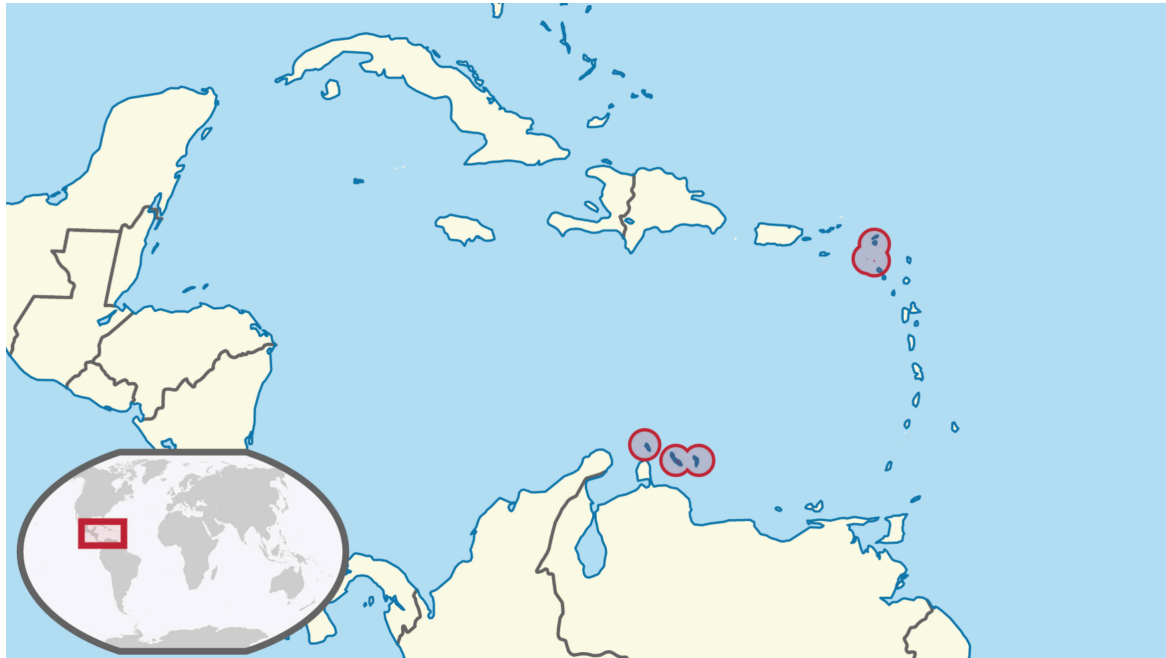
Figure 1. *Map of Dutch Caribbean islands. Source: Dutch Caribbean Species Register. Note the sheltered locations of Aruba, Curaçao, and Bonaire to the SW, and the exposed position of Saba, St. Eustatius, and St. Maarten to the NE.*

DATASET CONSTRUCTION

Focusing on marine islands impacted by hurricanes, data was compiled on the Dutch Caribbean islands of Aruba, Bonaire (and Klein Bonaire), Curaçao (and Klein Curaçao), Saba, St. Eustatius, and St. Maarten in order to test the model against a realistic scenario. They are represented in the map in Figure 1. These islands were specifically selected because of the consistent biodiversity data present in each of them, and because of the islands' variability in their tendency to experience hurricanes. Insular species richness was compiled from the Naturalis Biodiversity Center's Dutch Caribbean Species Register (dutchcaribbeanspecies.org); unicellular and aquatic species were excluded from the search. Additionally, Google Maps was used to measure island area and distance from the mainland, where the mainland is assumed to be South America for all the islands. It is noteworthy that northern South America's total species richness is yet unknown, but an estimate of $P = 100,000$ was deemed appropriate based on world terrestrial multicellular species richness estimates (Caley et al., 2014). Dispersal and disturbance parameters (f and *h*) were calculated according to data found on the Caribbean Hurricane Network's Climatology of Caribbean Hurricanes, for each specific island (stormcarib.com). The dataset thus compiled on the Dutch Caribbean islands is presented in Table 3.

Island	Mainland	s	P	S	Dist. (km)	Area (km²)	d	A	f	h
Aruba	S. Am.	893	100000	0.00893	27	193	1.20	1.48996	0.635	0.3175
Bonaire	S. Am.	892	100000	0.00892	87	294	1.78	3.45744	0.565	0.2825
Klein Bonaire	S. Am.	49	100000	0.00049	95	6	1.86	0.00144	0.565	0.2825
Curaçao	S. Am.	1466	100000	0.01466	66	444	1.59	7.88544	0.565	0.2825
Klein Curaçao	S. Am.	48	100000	0.00048	64.5	1.7	1.58	0.00012	0.565	0.2825
Saba	S. Am.	1644	100000	0.01644	780	13	8.02	0.00676	7.22	3.61
St. Eustatius	S. Am.	1416	100000	0.01416	760	21	7.84	0.01764	6.34	3.17
St. Maarten	S. Am.	1275	100000	0.01275	430	87	4.87	0.03028	6.09	3.045

Table 3. *Dutch Caribbean species richness and insular parameters. Data derived from Naturalis (2020) and stormcarib.com (2020).*

FUTURE CONDITIONS

In order to model future species richness on the islands in question, it is necessary to calculate new dispersal and disturbance parameters for the islands in a future scenario. The future time period referenced throughout this paper is conceptualized as the year 2100 with a 2°C mean global temperature rise from 2000, based on the Intergovernmental Panel on Climate Change's fifth synthesis report (Pachauri et al., 2015). In this scenario, hurricanes and other tropical cyclones are expected to increase in intensity by 2-11%, while frequency is expected to decrease by 6-34%. There is "less confidence in future projections" of the latter metric. (Knutson et al., 2010; NOAA, 2020) Precipitation rates associated with hurricanes are expected to increase ~15% (Pachauri et al., 2015). Predictions in this paper are calculated based on the greatest percentage change within acceptable confidence intervals, namely, an 11% increase in intensity and a 6% decrease in frequency. The projected increased precipitation rate is not considered within the dispersal or disturbance parameters, as the measurement is relatively fine-grained.

Model construction and implementation and plot output was executed through R (v4.0.3), utilizing the 'deSolve' package for ordinary differential equation calculations and the 'ggplot2' package for graphics creation. Least square minimization was performed through the 'optim()' function, optimizing through the Nelder-Mead algorithm.

RESULTS

Adjusting the floating parameters to best fit the model to the observed data presented, the parameters' values were calculated as follows: $\alpha = 10$, $\beta = 5755.59$, and $\gamma = 9.85$, resulting in the following equation:
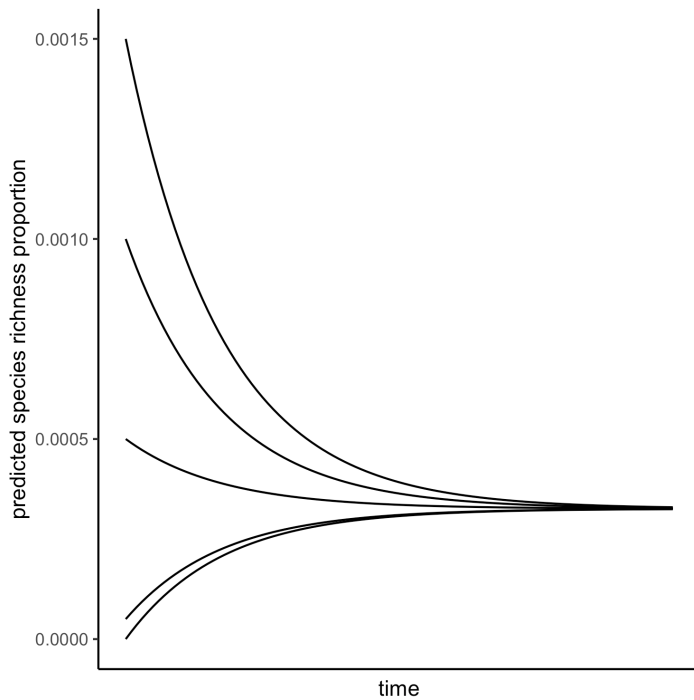
Figure 2. *Plot of species richness behavior over time, beginning at different initial states. Starting at different initial states, and given identical parameters, each trial approaches the same equilibrium. In this case, parameters are d=9, A=1, f=1.2, and h=0.6.*

$$\frac{dS}{dt} = 10\left(\frac{1}{d} - \frac{S(t)}{d}\right)\left(\frac{f}{f+1}\right) - 5755.59\left(\frac{S(t)}{A}\right) - 9.85\left(\frac{h^2}{h^2+1} - 1\right)$$

The behavior of species richness proportion is observed over time ($S \sim t$), reaching equilibrium starting at multiple initial states in Figure 2. Initial state is shown to have no effect on the ultimate equilibrium species richness proportion of the island in question. Even a hitherto uncolonized island ($S_{initial} = 0$) approaches the same expected equilibrium as previously colonized islands of identical parameters.

Using the dataset presented in Table 3, predicted species richness at equilibrium ($\tilde{S}$) is plotted against the observed species richness of the islands (σ) in Figure 3. Though predicted values consistently fall within the same range as the observed values, it is of note that the three islands of Saba, St. Eustatius, and St. Maarten are predicted to have much scarcer species richness than they do, and this is potentially owing to their significantly different climate patterns

Island	Modeled value	Scalar correction	Observed value
Aruba	0.003151578	2.83350119	0.00893
Bonaire	0.006689898	1.33335366	0.00892
Klein Bonaire	0.000002769	176.959191	0.00049
Curaçao	0.015542120	0.94324326	0.01466
Klein Curaçao	0.000000229	2096.06987	0.00048
Saba	0.000002111	7787.7783	0.01644
St. Eustatius	0.000006110	2317.51227	0.01416
St. Maarten	0.000014322	890.238793	0.01275

Table 4. *Scalar corrections between observed and modeled insular species richness proportion.*
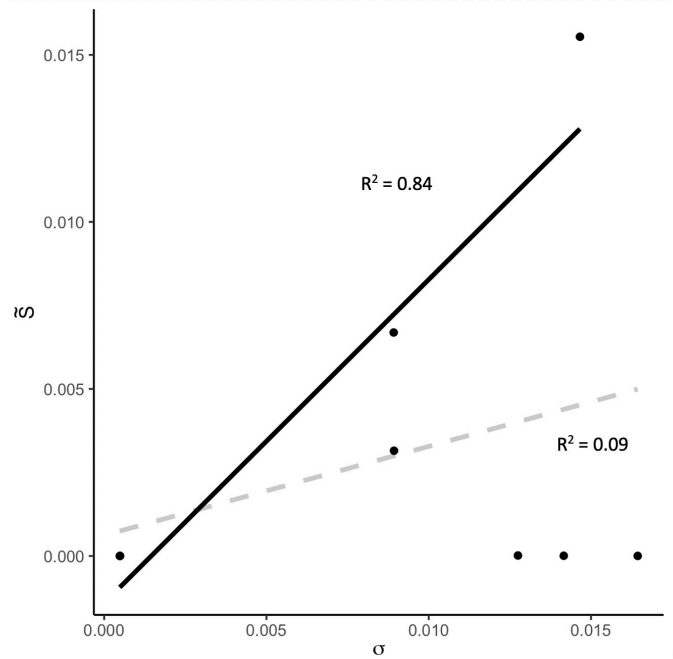

Figure 3. *Plot of predicted versus observed insular species richness proportions.*

Island	Present observed richness (s)	Predicted future richness (s)	Percent Change
Aruba	893	874	−2.15%
Bonaire	892	874	−2.08%
Klein Bonaire	49	48	−2.11%
Curaçao	1466	1437	−1.99%
Klein Curaçao	48	47	−1.97%
Saba	1644	1463	−11.02%
St. Eustatius	1416	1239	−12.46%
St. Maarten	1275	1152	−9.63%

Table 5. *Expected changes in species richness based on dispersive model predictions. Note: Numbers in "predicted future richness (s)" column are rounded up to the nearest unit.*

than the rest of the islands. Whereas the other islands considered are tropical arid, Saba, St. Eustatius, and St. Maarten are dominated by tropical rainforests. Removing the three islands' data points from analysis, R^2 increases from 0.09 to 0.84. Nevertheless, scalar corrections between the observed and predicted values are presented in Table 4.

After the application of future climate condition parameters to each island, the insular species richness proportion of the islands are plotted in present and future condition in Figure 4. Owing to the islands' small size, Klein Bonaire, Klein Curaçao, Saba, St. Eustatius, and St. Maarten are plotted once more below the main plot in Figure 4, each to an appropriate scale. The islands uniformly experience a decrease in species richness under future conditions. The model's predictions are corrected and reverted from proportion to absolute richness, leading to the actual decrease in species number expected on each island, as presented in Table 5. The islands more sheltered from hurricanes in the present (Aruba, (Klein) Bonaire, (Klein) Curaçao) are predicted to experience a decrease of ~2% in species richness, whereas the islands that are presently more exposed (Saba, St. Eustatius, St. Maarten) are expected to experience ~9-13% decrease in species richness, leading to predictions of significantly greater alpha diversity loss on the latter islands.
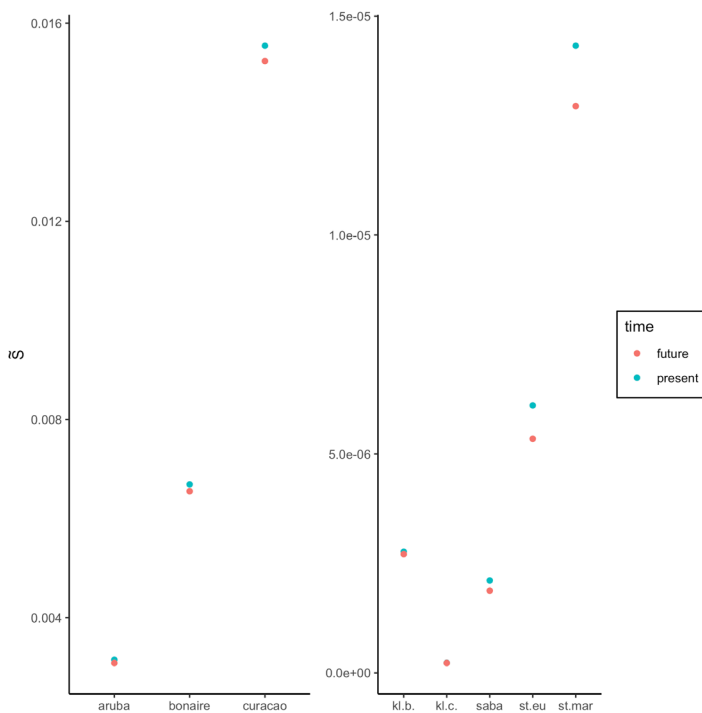
Figure 4. *Plot of modeled present versus future insular species richness.*

DISCUSSION

It is of note that the model as constructed presents a relationship between the scalar correction factors and island size. The scalar correction factors, used to equate the model predictions to observed data, generally decreased with increasing island area, as presented in Figure 5. This indicates that larger island sizes produce smaller discrepancies between model results and observed data, requiring less correction. This discrepancy may further support a behavioral devolution into chaos within the system, once a small enough island area threshold is crossed.

Observing future species richness equilibrium predictions (Figure 4, Table 5), in tandem with the current understanding of global climate change patterns, it is unsurprising that islands are expected to see a significant decrease in species richness. It is apparent that Saba, St. Eustatius, and St. Maarten are expected to experience a greater loss in diversity. This may be best explained through these islands' geographic location in relation to the hurricane belt (the general trajectory of North Atlantic hurricanes): the islands fall within this hurricane belt, leading to larger climate-mediated hurricane effects on the islands. In other words, the fact that these islands experience more hurricanes signifies their increased sensitivity to a change in hurricane disturbance levels (h).

Moreover, the similar trends of sharp decline on the three islands may be further explained through the saturating effect of the dispersive parameter, f, and the sigmoid function of the disturbance parameter, h. Seeing as $\frac{dS}{dt} \sim \frac{f}{f+1}$ and $\frac{dS}{dt} \sim -\frac{1}{h^2+1}$, and holding $h = \frac{f}{2}$ constant, as has been assumed throughout this paper, the interactions of these two parameters leads to the following trend:

$$\tilde{S} \sim \frac{f}{f+1} + \frac{1}{\left(\frac{f}{2}\right)^2 + 1}$$

The trend above produces a curve with a local maximum, which suggests that, at certain f and h values, species richness increases before decreasing significantly. Because the islands of Saba, St. Eustatius, and St. Maarten have higher dispersal and disturbance parameter values than the rest of the islands, they may be closer to this species richness maximum in present conditions (see Figure 6). These values, along with the islands' wetter and more forested habitats, may explain their high species richness numbers. Moreover, the islands' sharp decline in species richness, as predicted for future conditions, is best conceptualized through being pushed beyond the curve's maximum.

As described above, the islands of Saba, St. Eustatius, and St. Maarten showed a large discrepancy in real versus modeled values of insular species richness. This discrepancy may be best attributed to the islands' wetter climate, leading to the need for differential calibration of the floating parameters α, β, and γ based on these islands significantly different macrobiotic regime. Additionally, the islands' location within the Lesser Antillean chain of islands puts them in close proximity to insular sources of colonization, otherwise known as internal colonization, which had been excluded from this model. The importance of internal colonization is empirically supported by several examples—for instance, the presence of a ring species complex in *Euphorbia tithymaloides* (order: Malpighiales), solidifying through evolutionary diversification the island-to-neighboring-island colonization pathway in the Caribbean (Cacho & Baum, 2012).

In contrast to Saba, St. Eustatius, and St. Maarten's higher hurricane frequency, the islands of Aruba, (Klein) Bonaire, and (Klein)
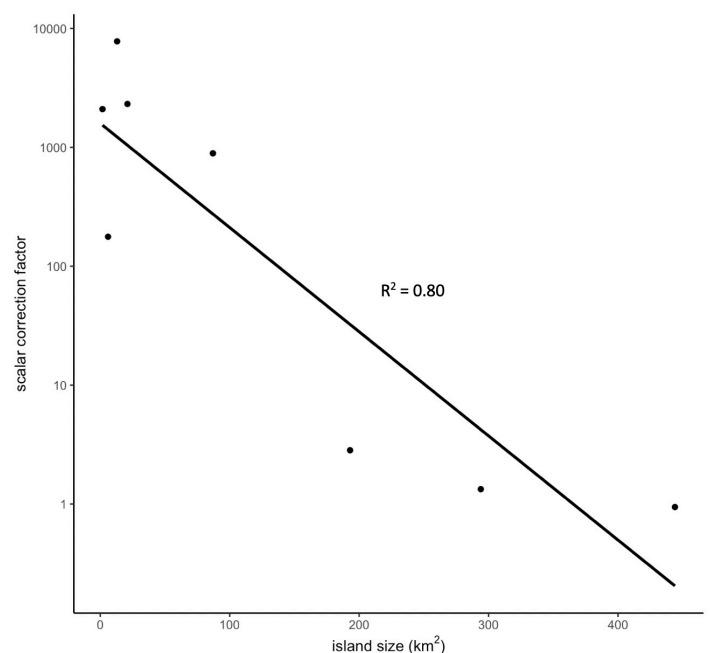

Figure 5. *Plot of scalar correction factors against the island size (km²).*
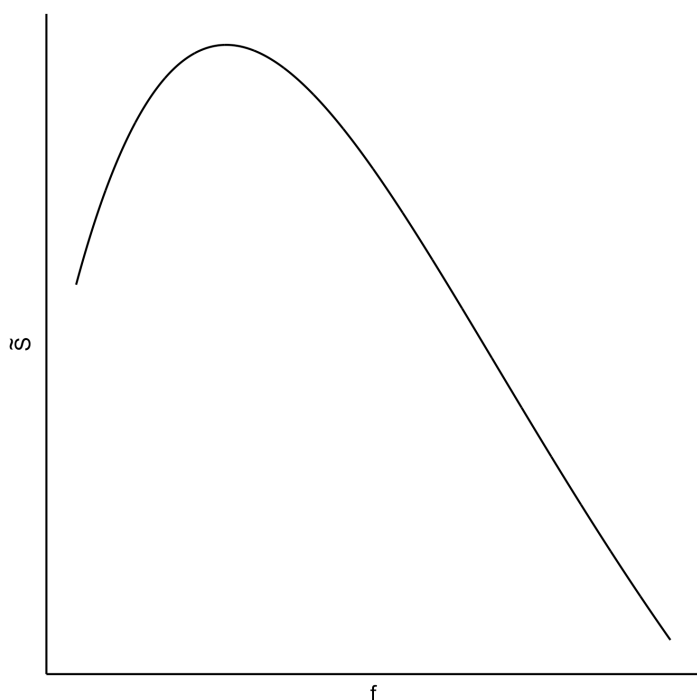
Figure 6. *Plot of equilibrium values of insular species richness over a range of dispersal parameter (f) values.*

Curaçao, are situated at relatively safe geographic locations in terms of hurricane probability. As such, even with the same percent increase in hurricane intensity, and with the same percent decrease in hurricane frequency, these islands are not predicted to suffer diversity losses comparable to the former group of islands.

Although the predictions described in the result section above prove helpful for understanding the patterns of species richness change in a future scenario with more intense and less frequent hurricanes, these results may be far too conservative. As significant sea level rise and an increase of up to 20% in hurricane-associated precipitation is expected by the year 2100, permanent and seasonal inundation may leave current terrestrial habitats decimated (GFDL, 2020; Knutson et al., 2010; Pachauri et al., 2015). Additionally, changes in weather patterns and increased air temperatures may further worsen the effect. To account for these changes, more realistic future predictions would increase the disturbance parameter (h) at a much higher rate than the dispersal parameter (f), instead of maintaining a constant relationship ($h = \frac{f}{2}$).

Process-based mathematical models, such as the one presented in this paper, may prove useful or even crucial in better assessing and managing ecosystem resources in the future (Cuddington et al., 2013). Nevertheless, hurricanes (and climatic events in general) produce significantly different effects based on the organism, ecosystem, or island in question (Tanner et al., 1991). Thus, general biogeographic models in this vein cannot be exact, yet their generalist nature can guide the user to larger and more coarse-grained patterns that are in helpful in their very lack of specificity.

Moreover, the dispersive force model presented above has great applicability in answering questions of biogeography concerning other ecological islands. With the understanding that hurricanes represent one example of climatic events, future directions would

entail constructing a system to measure and categorize disturbance and dispersal magnitudes across different types of climatic events (e.g. wildfires, tornadoes, marine currents, floods, etc.), based on their respective frequencies and intensities, in order to study the biogeographic effects of climatic events in other island systems, including montane islands, reefs, and bodies of water.

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ABOUT THE AUTHOR

Anthony Sarkiss,
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by Max Heimowitz, Benjamin Franklin '23

Anthony Sarkiss is fascinated by connection and change: the connections between the small and large, from molecular biology to biospheric data, and systems thinking, determining the ecological drivers of change and locating areas of resistance. A senior E&EB major in Pauli Murray college, Sarkiss is a certified scuba diver and has conducted research since the summer of his first year at Yale—first in the Jacob Lab and now the Edwards Lab.

Sarkiss became interested in ecology when he was in high school, having spent time working in a botanical garden and participating in his school's scuba club. He was involved with the Surfrider Foundation in Miami, where he calls home, contributing to dune and coral restoration efforts. At Yale, Sarkiss has both volunteered and worked for the Marsh Botanic Gardens greenhouse since his first year, in addition to being a member of the Community Health Educators and the Arab Students Association.

Sarkiss has immersed himself in research not only in the classroom—by taking field-based classes, studying local forests and lakes in Connecticut—but also by working in the lab. As the only under-graduate student to enroll in the graduate course "Mathematical Models and Quantitative Methods in Evolution and Ecology," Sarkiss was initially wary, yet also excited by the freedom he found in shaping his studies. Whereas graduate students used the class to build models related to their own interests, Sarkiss did not have any particular question or area of study on which he sought to focus; he simply "picked a cool question and was able to run with it." Sarkiss was then able to study the effects of climate change—in particular, of hurricane frequency and intensity—on species richness and diversity in ecological islands in the Caribbean, after having created a model in this graduate course. Enrolling in a graduate-level class as an undergraduate really served to demystify the expe-rience for him, as it was not as daunting as he had initially thought.

Sarkiss has found guidance, support, and open communication channels every step of the way in his research work, and his experience in the lab has shown just how much his interests in biology hold true. There is a difficulty inherent in the interdisciplinary biology he has aspired to study as an undergraduate student, especially in how the departments are split up, making it tougher to answer the questions that he seeks to pose. Not a "lake person" or "bird person," he hopes to take some time off after graduating in the spring in search of something that will best match his interests.

For the full-length profile, visit yalesymposia.com