Research Article

Simulating Species Richness Using Agents with Evolving Niches, with an Example of Galápagos Plants

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I sought to evolve plant species richness patterns on 22 Galápagos Islands, Ecuador, as an exploration of the utility of evolutionary computation and an agent-based approach in biogeography research. The simulation was spatially explicit, where agents were plant monocultures defined by three niche dimensions, lava (yes or no), elevation, and slope. Niches were represented as standard normal curves subjected to selection pressure, where neighboring plants bred if their niches overlapped sufficiently, and were considered the same species, otherwise they were different species. Plants that bred produced seeds with mutated niches. Seeds dispersed locally and longer distances, and established if the habitat was appropriate given the seed's niche. From a single species colonizing a random location, hundreds of species evolved to fill the islands. Evolved plant species richness agreed very well with observed plant species richness. I review potential uses of an agent-based representation of evolving niches in biogeography research.

1. Introduction

In biogeographical analyses of island species richness, the number of species on each island is typically compared with island area, the distance between island centroids, and other variables using regression. Colonization, speciation, extinction, and dispersal are subsumed in the analytical models (i.e., mathematical models with simple closed-form solutions or approximations [1]). The equilibrium theory of island biogeography [2, 3] has been profoundly important in advancing understanding [4], and the theory has been modified, extended (e.g., [5, 6]), and critiqued (e.g., [7]).

Analytical approaches have advantages and disadvantages. They are straightforward and provide precise and rapid results, but the analytical solutions may not hold for more complex or less stylized situations. The opposite is true for simulation modeling (i.e., difference equation models simulated by computer [1]). Formulation of a simulation model can be complex, multiple simulations are required to improve precision and interpretation can be difficult, and simulations can be computer intensive. A main advantage of simulation modeling is its flexibility. Contextually specific and realistic simulations may be easily made, and conditions altered in experimentation [8]. Also, variation between population members is easily included in simulations. Lastly, advancements in computational capacities and speed, and in the flexibility of modeling platforms and programming languages, have sped development and simulations [9].

To varying degrees, advances have allowed researchers to model with the realism and precision that Levins described [10], without the sacrifice in generality he cited, because of an ability to now do simulations at broader spatial or temporal scales. The approaches can be complementary, each providing unique insights [11]. Simulation approaches remain rare in biogeography research [12].

In island biogeography theory, island area, maximum island elevation, and related measures are surrogates for habitat complexity or the number of niches available [13–17], with more diverse areas able to support more species [18, 19]. Hutchinson's [20, 21] representation of niches as n-dimensional hypervolumes has been criticized [22], but the concepts have been widely applied, such as in niche

theory (e.g., [22–25]) and modeling [12, 26–29]. On any niche dimension (e.g., mean temperature), the tolerance of an organism will vary, so that over some portion conditions will be optimal, over other portions conditions will be suboptimal, and the species cannot exist over some portions of the dimension [30]. Combining niche dimensions yields a fundamental niche volume of potentially suitable habitat for a species, from which a smaller niche volume will be realized. Competitive exclusion [31–33], limiting similarity [32, 34], and ecological release [35] promote niche differentiation, and, through this and other forces (geographic separation, genetic drift, mate choice, polyploidy, etc.), speciation.

Field work and analytical modeling have been used for decades to improve our understanding of community structure and change. More recently, simulations have been used to emulate changes in niches (e.g., [12, 36, 37]) and speciation [12, 38–43]. Agent-based simulation modeling features autonomous entities that interact with their environments and each other, working toward some goal [44]. Agent-based simulation is popular in social sciences [45], but is gaining use in ecology [46–49]. I use the term agent-based simulation here, rather than individual-based simulation, to emphasis the importance of interactions between agents in what follows. Another technique gaining use in ecological fields [12, 50–55] is evolutionary computation [56]. In evolutionary computation, hundreds of potential solutions or organisms compete to optimize an objective function, with the best adapted producing offspring with related but mutated characteristics and the least adapted removed from the population. Over many generations, the population evolves to better fit whatever objective function is of interest, such as a design constraint or reproductive fitness.

Critiques of island biogeography theories often focus on how the complexities of islands are ignored [57] and that speciation was excluded from the original model [4]. I sought a simple model, where in a simulation the observed number of plant species on islands would evolve from a single species, using more direct measures of habitat complexity (i.e., topographic variation) than simple area measures typically used in biogeography analyses. I applied to the Galápagos Islands an agent-based model of plant population dynamics that incorporated competitive exclusion and limiting similarity based on space, time, and niche overlap. The model simulated adaptive radiation into unexploited niches yielding many monophyletic species.

Two approaches are highlighted in these analyses, agent-based modeling and evolving niches. These approaches are distinct, and their utilities may be judged separately. The use of evolving niche dynamics in biogeographical research is specialized, but I believe an intriguing pathway toward discovery. But I am more confident of the utility of agent-based modeling featuring interacting agents in biogeography research. As computer processing power and speed steadily improve, we are increasingly able to simulate process-based interactions and movements of organisms in systems, regions, and across the globe. Simulations incorporate biogeographic hypotheses in a spatially explicit manner, and then the flexibility of the approach may be exploited to assess those hypotheses using scenario analyses [8].

2. Application Area

Since Darwin's voyage more than 170 years ago, the Galápagos Islands have served as a test-bed for biogeographical theories. The volcanic islands 930 km from mainland Ecuador have been populated by dispersers most often of American origin [58]. For example, pteridophytes, such as spore-producing ferns, had frequent immigrations and evolution within the archipelago played a minor role in creating their island diversity [59, 60], but spermatophytes (seed producers) more often evolved through sympatric, parapatric, and allopatric speciation [61]. Botanical surveys yielded lists of plant species occurring on the islands, from which species richness has been tallied for each of the main islands (e.g., [62]). Indigenous (i.e., not introduced by humans) vascular plant species richness on the Galápagos Islands (Figure 1) has been associated through regression analyses with island area, area modified to exclude lava flows, maximum elevation of islands, and distance to neighboring islands [13, 15–17, 60, 62–68]. Later analyses using surveys [69] that include at least 95% of plants on large islands [70] often yielded good agreements between biophysical attributes and plant species richness.

3. Methods

3.1. Overview. In the agent-based model, the Galápagos Islands and ocean of the archipelago were represented as cells. Entities in an agent-based model were represented by plant monocultures, with ≤1 species occupying each of the cells. Any cell with plants was occupied by many individuals grouped into a single agent, but for brevity I will refer to the agents as plants. Plants were represented by three niche dimensions: two were unimodal based on elevation and slope, and a third was whether the land was soil or unsuitable lava [17]. A single species colonized a randomly selected patch of soil. In a repeating cycle, neighboring plants bred if their niches overlapped sufficiently and produced seeds with niches that included slight mutations. If a neighboring cell was empty and had suitable habitat based on the seed's niche, the seed germinated. Seeds also dispersed, and if the destination habitat was suitable, a seedling was established. Colonization of islands in the archipelago was by direct seed dispersal and by stepping-stone dispersal [2, 58, 62]. Dispersal was modelled as occurring in random directions and a declining probability with distance; in reality birds are the most common dispersers on the Galápagos Islands [66]. Numbers of species per island were tallied, with species differentiated based on the overlap in species niches. Several simulations with random colonization sites were conducted in exploratory and sensitivity analysis. Mean numbers of plant species for islands from simulations were compared to the observed numbers of plant species using correlation analysis. Individual islands were then removed, and simulations repeated, to partition the contribution of each island to the richness on the remaining islands.

3.2. Niche Representation. Niches were represented as multi-dimensional hypervolumes defined by elevation, slope, and
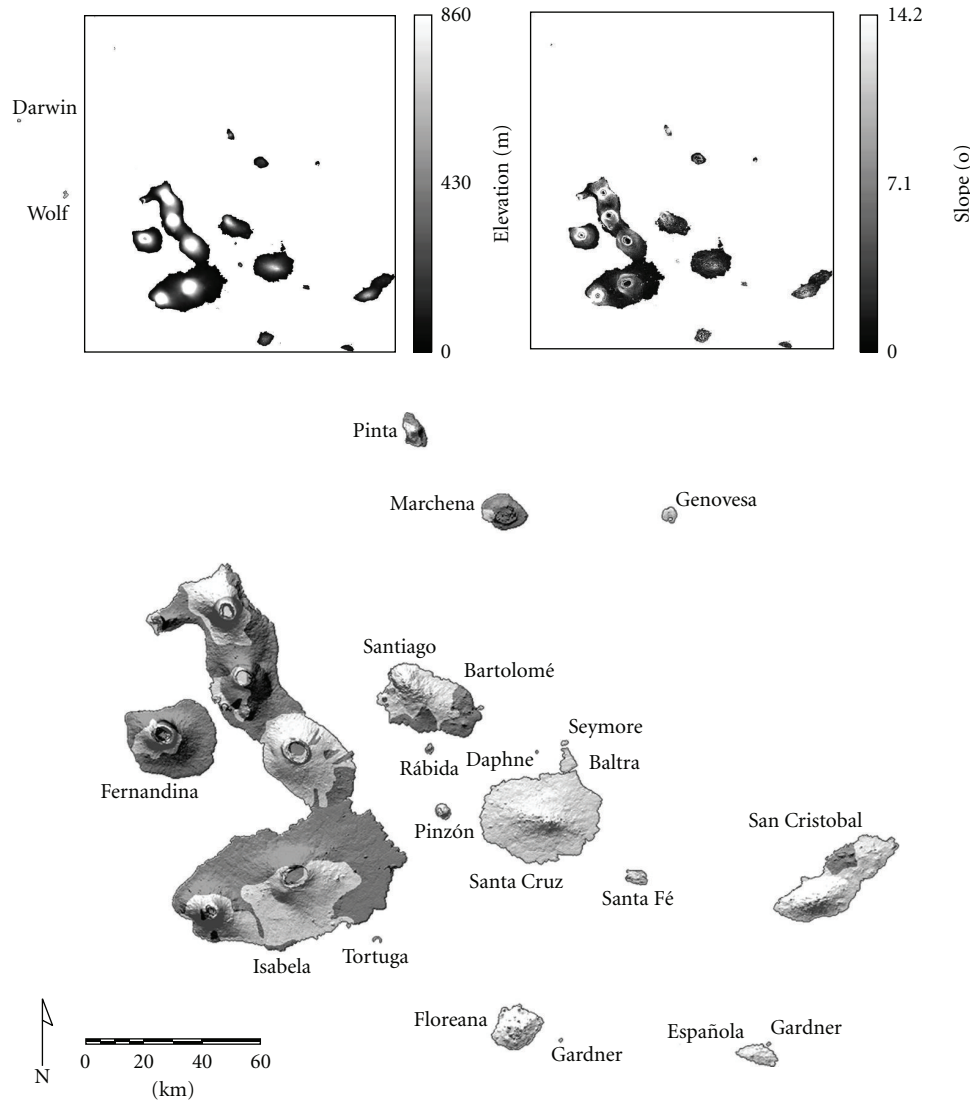
FIGURE 1: The islands of the Galápagos Archipelago used in analyses ($n = 22$). Topography is in shades of grey, with lava flows in darker shades. Insets show elevation and slope, with upper ranges defined by the mean plus twice the standard deviation.

the presence or absence of soil. Lava flows (Figure 1) were not suitable for plant establishment [17], and seeds that dispersed into cells representing ocean were lost, so only cells representing soil were suitable habitat. Lava was a simple binary response in determining habitat suitability. It may be intuitive to use spatial surfaces thought to be closely tied with competition and adaptation in plants, such as, temperature, precipitation, soil moisture, soil fertility, and drainage. However, surfaces such as those were not available at the high resolution I sought. Instead, surrogates that were available at high resolution were used to define the remaining niche dimensions, namely, elevation and slope. Elevation and slope are not perfect surrogates for the attributes cited, but they do serve to define habitat diversity more precisely than what is traditionally done using island area, for example. Elevation spanned from 0 to 1704 m, and slope from 0 to 82 degrees. I standardized these surfaces for several reasons:

to make the niche dimensions more comparable, to allow the values to be stored as eight-bit integers, and to simplify advanced calculation of the overlap of niche dimensions, expanded upon below. Elevation and slope were therefore multiplied by constants to yield resulting surfaces with values that spanned the same range, from 0 to 255.

Niche dimensions were represented with unimodal utilization functions defined by unit normal curves, so that only two parameters, mean and standard deviations, defined each curve [32, 34, 37, 71–73]. A species with a broad niche width (e.g., $N(\mu = 128, \sigma = 50)$ on a dimension stretched from 0 to 255) was adapted to a broad range of environments, at least relative to that niche dimension. A species with a narrow niche width $[N(128,5)]$ was adapted to a limited portion of that niche dimension (Figure 2(a)). My use of unit normal curves was important; the area under the curve was constant (discussed by Ackermann and Doebeli [37]
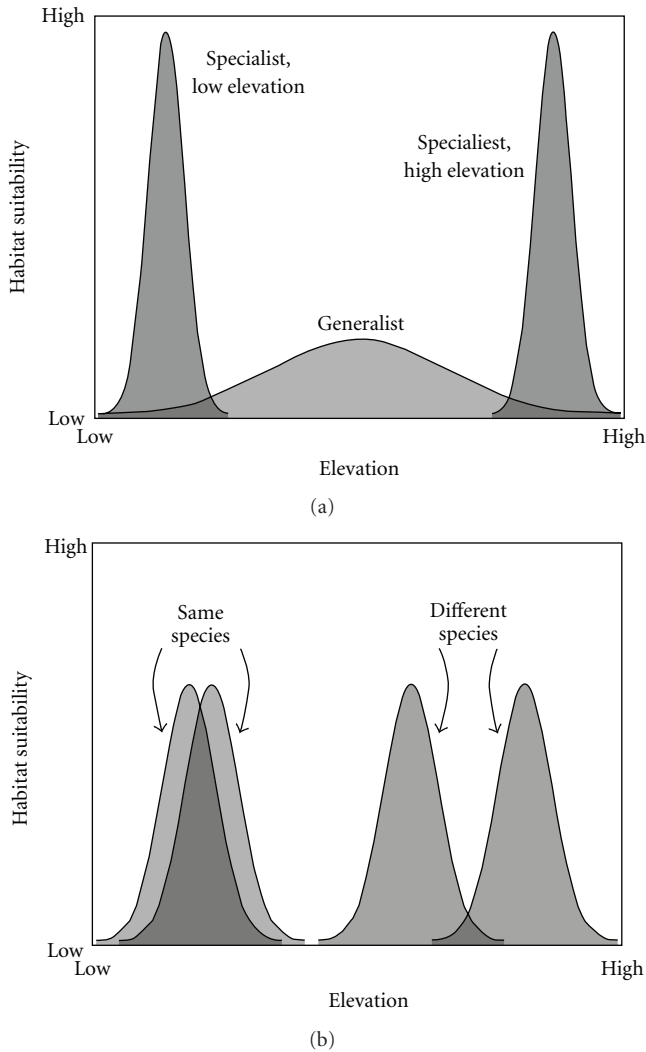
(a)

(b)

Figure 2: A schematic demonstrating plant species niche spaces, showing (a) specialists and generalists relative to elevation. Specialists have small standard deviations in niche dimension and generalists have large standard deviations. Plants with niches that overlap (b) sufficiently in niche dimension are considered the same species and are able to breed. Plants with niches that do not overlap sufficiently are separate species.

Table 1: A summary of the parameters in the model, grouped into classes, their values, and their units. Values used were determined through exploratory analyses.

Class	Parameter	Value	Units
Niche relationships			
	Overlap in elevation	0.75	Proportion
	Overlap in slope	0.79	Proportion
	Habitat suitability coefficient	1.26	—
Mutations			
	Rate of mutation	± 0.33	Probability
	Mean	6	Niche units
	Standard deviation	4	Niche units
	Rate of rare mutation	± 0.01	Probability
	Mean	25	Niche units
	Standard deviation	12	Niche units
Long-distance dispersal			
	Dispersers per breeding	7	Seeds
	A coefficient	500	Cells
	B coefficient	0.002	—
Others			
	Age of plants	12	—
	Cycles modeled	800	—

patch was suitable for seedlings to germinate. In the first case, plants with niche dimensions that overlapped sufficiently in both elevation (i.e., 75% overlap, derived from exploratory analyses to maximize agreement with observed richness, Table 1) and slope (79% overlap) were classified as the same species, otherwise they were separate species. Only plants that were the same species and in adjacent cells bred, and created seeds assigned niche dimensions that were averaged values of the parent plants. Seeds did not establish in habitats outside their niche hypervolumes. For each of the habitat dimensions (elevation and slope), the value for the land where the seed may establish was used in a query (an X value) returning the height of the normal curve for that dimension of the seed's niche (a Y value), which was multiplied by a constant, 10,000. The likelihood that seeds would germinate in a given habitat type was adjustable; a parameter (1.26, Table 1) was multiplied by the Y value before comparing the result with the Y value returned. If the habitat was inappropriate in either dimension (elevation or slope), the seed did not germinate.

3.3.2. Mutation of Niches. The niches assigned to some seeds were mutated so that plants evolved to populate new habitats. The means and standard deviations of niche spaces were tested independently; with a one-third chance (Table 1), a mutation value would be added to the niche dimension, and with an equal chance the value would be subtracted. In rare cases (1 in 100, Table 1), niches were mutated by larger values to speed the adaptation of plants and increase the likelihood that unique habitats (e.g., steep slopes) would be colonized. This rare mutation may be thought to include hybridization,

and Day and Young [74]), so that plants could be very good competitors over a narrow range of niche dimension ($N(128,5)$—specialists), or poorer competitors but over a broad range of a niche dimension ($N(128,50)$—generalists). The mean of niche dimensions shifted as well. For example, some plants were adapted to gentle slopes ($N(5,20)$) and some to steep slopes ($N(240,20)$) (Figure 2(b)).

3.3. Model Parameters. Model parameters are shown in Table 1, grouped into classes that are discussed below.

3.3.1. Niche Relationships. I used niches in modeling in two ways: (1) to identify if plants that might breed were the same species and (2) to identify whether a given landscape

an important source of variation in island populations [75]. The means of niche dimensions were not allowed to drop below 0 or exceed 255, and standard deviations were limited to between 1 and 60.

3.3.3. Dispersal of Seeds.

I used two types of dispersal in modeling, one short-range, where plants that bred had seed that attempted to establish on one (and only one) neighboring cell, if the cell was empty. Plants also produced seeds (7, Table 1) that dispersed longer distances. A point in the study area was randomly selected, and the distance from the breeding pair of plants calculated. The probability of dispersal to that distance was calculated based on a power function [76]:

$$p = a^{-b \cdot d},   (1)$$

where a controlled the overall distance of dispersal, and b the shape of the dispersal curve, here essentially the rate of decline in numbers of seeds dispersing through distance. If a uniform random value was below p, the location was the site a seed dispersed to (although most often ocean or lava), otherwise a new location was selected and the next seed tested.

3.3.4. Others.

The time-step used in modeling was not associated with real time. Plants survived 12 time-steps (Table 1). In each simulation, 800 time-steps were modelled. That period was selected because it enabled the islands to fill with plants and reach some stability in species richness. The number of time-steps modelled does not relate to island history in any way.

3.4. The Simulation and Analyses.

I used a digital elevation model produced from the Shuttle Radar Topography Mission of 2000 [77] to characterize elevation and slope on the islands, which has a vertical error specified as <16 m globally [78]. The digital elevation model was composed of cells representing 92.5×92.5 m of land or ocean. The region modelled was 3499 columns and 3884 rows (323.7 km E-W, 359.3 km N-S). I used the map in Willerslev et al. [17] and a MODIS satellite image from May 2003 I had georectified to map lava flows (Figure 1). The most complete source [16] for observed native plant species richness came from Harvey [62], which in turn is based on the works of Lawesson et al. [69] and Connor and Simberloff [67]. Island names are from Willerslev et al. [17], and areas and distances are from Johnson and Raven [64].

I programmed the agent-based model in FORTRAN, and conducted simulations on a local Linux multiprocessor cluster. Two techniques proved important to keeping simulation times reasonable. Calculating the overlap in niches of many thousands of plant pairs was slow. I sped simulations by calculated all possible overlaps between two standard normal curves with means spanning from 0 to 255 by 5 unit increments, and standard deviations from 1 to 60 by 2 unit increments, and wrote the results to a file. That file, with 2.43 million entries, was used by the agent-based model as a rapid lookup table for overlaps, with niches rounded to

the nearest increment prior to the test. Lastly, searching the eight neighboring cells of every plant to locate other plants to breed with or empty cells for seedlings was slow. I used a byte array to identify the neighbors of each cell. As a plant was added to the landscape, values were added to neighboring cells in the byte array (i.e., to cells in directions NW, N, NE, W, E, SW, S, SE, I added 128, 64, 32, 16, 8, 4, 2, and 1, respectively). The same values were removed from the array when a plant died. In a simulation, I therefore knew that a plant with a byte array of value 0 had no neighbors, one of 255 had all eight neighboring cells occupied, and a value of 192 (64 + 128) indicated a neighbor to the S and SE.

By definition, plants on the same landscape cell were the same species. To speed adaptation and speciation, plants on the same cell were not allowed to breed. Plants that bred had to occur on neighboring cells on the landscape. Therefore, during a simulation, two plants were placed on neighboring cells selected randomly, with their mean niche values equal to the habitat at that location, and their standard deviations equal to 40. Time-steps were then modelled in a repeating cycle. Each plant in the population was given the opportunity to produce seed each time-step, but I did not wish to provide some benefit to plants that bred first, so plant indices were randomized prior to each cycle and the indices were traversed in order. Then

   (i) plants with at least one neighbor attempted to breed with a randomly selected neighbour, the attempt was successful if their niches overlapped;

   (ii) the resulting seeds may have been mutated in one or both niche dimensions;

   (iii) if a space was available and the habitat was suitable, a seedling was established on a neighboring cell;

   (iv) long-distance dispersal attempts were made, and if the habitat was suitable, a seedling was established;

   (v) plants were aged; plants that exceeded the maximum age died, leaving the cell vacant.

A file storing the attributes of each plant location and its niche dimensions was postprocessed by a Visual Basic (ver. 6.0, Microsoft Corp., Redmond, Washington) program. That program mapped the results of each simulation for visual interpretation, useful in confirming simulation behaviour. The program compared the overlap in niche space for all the plants, and mapped species. In a first pass the averages of niche mean and standard deviations were calculated for all the plants. In a second pass, the overlaps between the average mean and standard deviations for each niche dimension were calculated for every plant, and those that overlapped sufficiently were labelled as a single species. The process then was repeated for the plants that had not yet been assigned a species identifier. That cycle continued until all plants had been assigned a species identifier. Lastly the program tallied the number of plant species on each of the islands in the Galápagos Archipelago.

My primary goal was to model species richness, and I used simple correlation to compare observed and simulated mean plant species richness on the islands. Spatial auto-correlation in richness between islands complicates tests of

agreement, but only general agreement is of interest here, and so P-values are not shown. Secondarily, I sought to have a similar total number of native plants observed and modelled across the archipelago.

In exploratory analyses, I identified the suite of parameters that best described species richness and the number of species observed (Table 1). I interpreted results from sensitivity analyses considering the biological role each parameter plays. To demonstrate one aspect of the flexibility of the general approach, I then quantified the contribution to plant richness within archipelago islands that each island made, by removing from the model each island in turn and noting changes to the species richness seen on the remaining islands. Simulations were conducted as described for the main model, except that plants present at the end of a simulation with all islands intact were saved to a file, then that file was used to initialize plants for each of these analyses (but plants were not placed on islands excluded from an analysis). That allowed the full 800 generations used in these simulations to model plant species on filled islands, with plant species richness waxing and waning in response to each new constellation of islands. Changes for the removed islands that caused significant differences in 12 or more of the remaining islands were illustrated, with the significant changes highlighted. Each set of analyses was simulated using multiple replicates, 60 for the main model, 24 for sensitivity analyses, and 50 for analyses partitioning contributions from individual islands to richness. Replicated simulations yielded mean numbers of plant species per island with small standard errors.

4. Results

In simulations, plants spread quickly from the single pair that colonized the Galápagos Islands, and secondary colonies appeared on neighboring islands through direct and stepping-stone dispersal. All the available habitats on the islands filled with plants within the generations modelled. Using the parameters from Table 1, the variation in observed plant species richness compared well with simulated richness ($r = 0.957$, 22 islands, 60 simulations) (Figure 3). Simulated species were not as widely distributed as in reality, with ca. 550 native species in the islands in reality [79], but 753 species modeled. This value (753) is in close agreement with the 749 angiosperms cited as on the archipelago by McMullen [80], but that number included observed plant species, subspecies, and varieties.

Elevation and slope interacted to create niche diversity. Unique niches promoted speciation, but the standardized elevation map included 183 unique values, and the standardized slope map included 186 values. Isabela Island alone has 428 species [62]. In analyses with the influence of elevation removed (i.e., overlap defining separate species set to 0), richness patterns based on slope alone still agreed well with observed richness ($r = 0.943$, 24 simulations), but only 176 species were modeled. When the influence of slope was removed and elevation was as in Table 1, agreement remained good ($r = 0.942$), but with 74 species modeled. Of course, removing the influence of both yielded
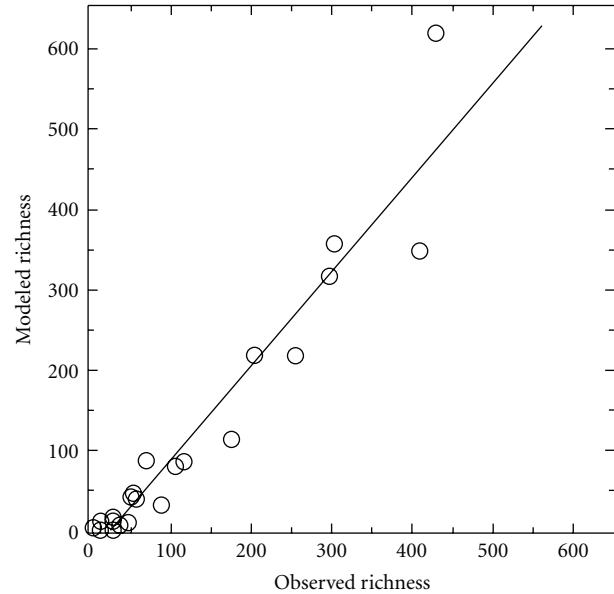

FIGURE 3: Modeled native plant species richness plotted against observe richness for 22 islands of the Galápagos Archipelago. A regression line provides reference ($r = 0.957$, 60 simulations).

a single species inhabiting the entire archipelago. Increasing the overlap parameters for elevation and slope beyond those in Table 1 increased the number of species modeled and reduced the agreement of simulated and observed richness. Reducing the habitat suitability coefficient (i.e., <1.26) reduced the number of seedlings being established and ultimately the number of species evolved, and the agreement between observed and simulated richness declined.

In sensitivity analyses, the rate and values of mutation most influenced the rate of speciation, rather than the overall fit of simulated and observed species richness. With no rare mutations (i.e., rate = 0 rather than 0.01), distinct habitats such as volcano rims were not populated and model fit was reduced. Setting the rate of rare mutation very high (e.g., 0.15) caused the fit of simulated and observed richness to decline ($r < 0.447$). Seedlings still could only establish on suitable habitat, but sufficient plants with extreme niche dimensions were established to escalate species richness on islands and decrease model fit.

The parameter controlling the shape of the dispersal curve (b) had little effect on model fit from 0.001 to 0.008. Small values led to a long tail in dispersal distances (e.g., at 0.002, 95% of dispersals were within 140 km, at 0.008, 95% of dispersals were within 40 km). Larger values decreased mean dispersal distances and model fit (e.g., $r < 0.71$ when $b = 0.014$, and 95% of dispersals were within 20 km), because islands distant from the colonizing island were unlikely to be colonized. Parameter a was set large (i.e., 500), and was not modified for simplicity; parameter b yielded sufficient flexibility to test effects of different dispersal distances. The number of dispersal attempts yielded a humped-shape relationship in variation explained, peaking at the value used (Table 1). With few dispersers (e.g., 1 or 2), islands were less likely to be colonized, there were fewer opportunities

for habitats to be occupied by well-adapted species, and model fit was poorer. With many dispersers (e.g., 10), plant species distributions were homogenized across the islands, and model fit was poorer.

The maximum age of plants affected model fit in a hump-shaped distribution as well. With plants surviving a few time-steps, many habitats were vacant, generalist species had many open habitats on which to establish, and plants were unlikely to form sustained populations on islands because two plants of the same species occupied neighboring cells less often. With plants surviving long periods (e.g., 30 time-steps), speciation was slowed and model fit was poorer when the number of time-steps modeled was as in Table 1.

Overall, the standard error across 50 simulations on estimates of richness when islands were prevented from being inhabited was <2% when the island was larger than Wolf (2.85 km^2). The maximum error was 9.5%, for Darwin. Few species on small islands make results more variable than for larger islands. In general, as expected, the effects of making islands uninhabitable on the richness on other islands was dependent upon their area and spatial arrangement. If small islands more distant from the center of the archipelago were uninhabitable (e.g., Darwin and Wolf), changes to richness on other islands were small. Marchena (129.49 km^2) and Floreana (170.92 km^2) are similar in area and distance from the center of the archipelago, but preventing plants from inhabiting Marchena had a modest effect on richness on other islands because the island is dominated by lava flows. In contrast, removal of Floreana led to notable changes in richness on other islands, and richness on Gardner near Floreana decreased by 11% when Floreana was unable to provide dispersing seeds. Removal of Genovesa led to a decline in richness on most islands smaller than Fernandina (634.49 km^2) and larger than Pinzon (17.95 km^2), with more idiosyncratic results for the smallest islands. This was a general pattern, that the largest islands had sufficient habitat abundance and complexity to maintain richness despite changes in the habitability of surrounding islands. Removal of the largest islands caused large changes in richness throughout the archipelago, as quantified below. However, preventing Fernandina from being inhabited caused few changes in richness on other islands. With much of the island in lava flows, and the island surrounded on three sides by Isabela, effects of it being uninhabitable were muted by the diverse and large populations on Isabela continuing to provide dispersing seed to other areas of Isabela and the remaining islands.

The removal of Isabela decreased plant richness in most of the remaining islands, with a 27 species decline in Santiago (Figure 4(a)). Removal of the next largest island, Santa Cruz, caused a decline of 3.8 species in Santiago and 4.5 in Santa Fé, but caused an increase of 3.8 species on Baltra (Figure 4(b)). The plants of that island, no longer receiving frequent dispersing seeds from Santa Cruz in this scenario, were sufficiently isolated to diversify more. Removal of Santiago also increased richness on the two largest islands, because of increased isolation (Figure 4(c)). The stepping-stone nature of dispersal in the model was evident when the small island of Tortuga was removed, which increased isolation and hence richness on Santa Cruz (Figure 4(g)).

5. Discussion

In simulations, a single pair of plants colonized a suitable patch of habitat within the Galápagos Archipelago and through adaptive radiation evolved into hundreds of species, with the number of species on the islands agreeing very well with the number of species observed (Figure 3). Because the model was spatially explicit, the aerial relationships that are part of classical island biogeography [2] were captured. Peripatric, parapatric, and allopatric speciation occurred, the radiation zones of [2] were evident, and species went extinct. As an example of parapatric speciation, a population would spread around the mid-elevations of a volcano. As it spreads, local conditions (i.e., elevation and slope) favoured the establishment of seeds with mutated niches. Differences in niche dimensions accumulated between plants within the wave-fronts moving in opposite directions; until upon meeting on the opposite side of the volcano, niches were so different the populations would not breed. Examples of allopatric speciation were more clear-cut, as the islands of the archipelago isolated populations, which allowed distinct niche dimensions to evolve [19]. The increase in species richness in some islands following the removal of a large neighboring island demonstrated adaptive radiation [81]. Moreover, the shapes and spatial arrangement of islands influenced rates of seed dispersal from one island to another and enabled stepping-stone dispersal [58]. Complex metrics that summarize distances between islands may [68] or more likely may not [82] aid in explaining species richness, but in the agent-based model, the entire archipelago is considered in dispersal. For example, Santiago Island may receive seeds dispersing from any island within the dispersal distance, but the likelihood of dispersal to Santiago declined with distance as in reality. The likelihood of dispersal to an island also declined with the size of the island of origin, not through any rule, but because fewer seed-producing plants occurred on smaller islands. The model includes some characteristics of species and their populations not captured by simple richness estimates, as encouraged by Connor and Simberloff [67]. The approach supports hypothesis testing. For example, these results are counter to Yeakley and Weishampel [68], who hypothesized high-elevation volcanoes would intercept dispersing organisms. Here intervening high-elevation areas did not affect dispersal from a given point, but simulated richness was in good agreement with observed richness. Lastly, typical biogeographic analyses have used surrogates for habitat complexity, whereas a more direct measure was used here.

Simulated richness on Isabela and Santa Cruz Islands did not agree as well with observed richness as for the remaining islands. On Isabela Island, 428 plant species have been collected [69], but my best model simulated 615 species. Willerslev et al. [17] considered Isabela to be composed of volcanoes separated by lava fields, which isolated them into five separate landscapes they used as separate entities in regression analyses. I attempted such an approach, but model fit was poorer. Two volcanoes on Isabela exceed 1650 m in elevation and include steep slopes—the number of niches available was extremely high [83]. In the model, plants
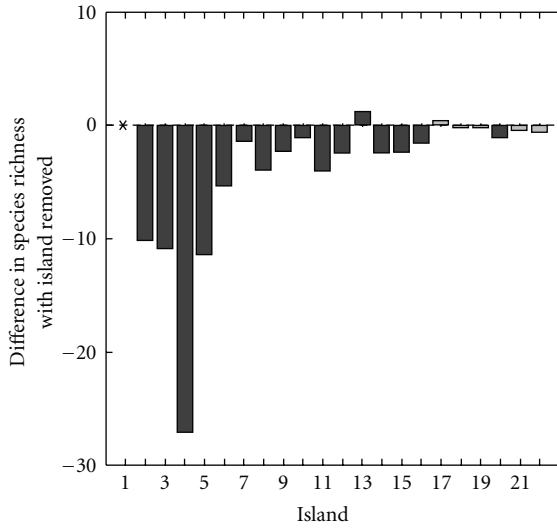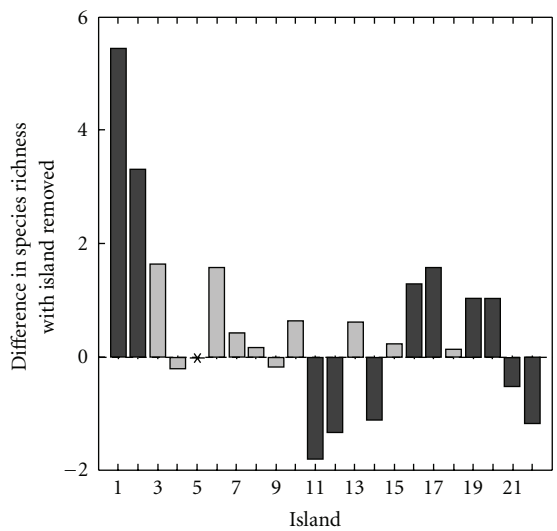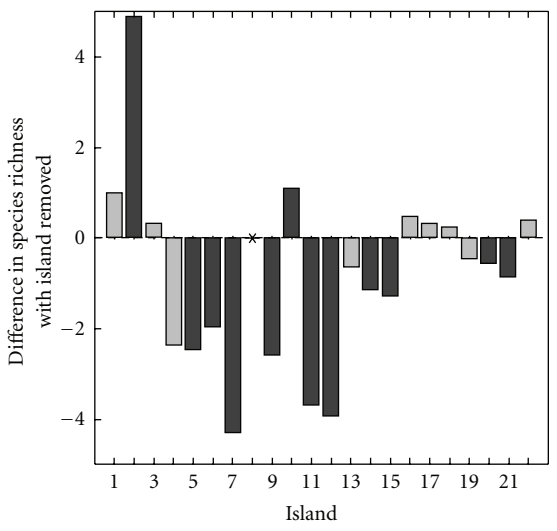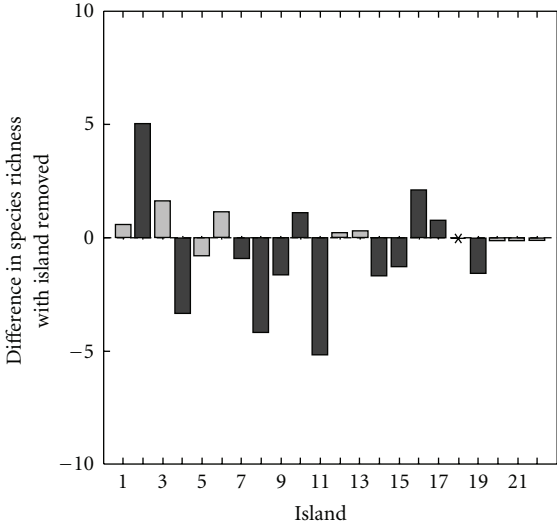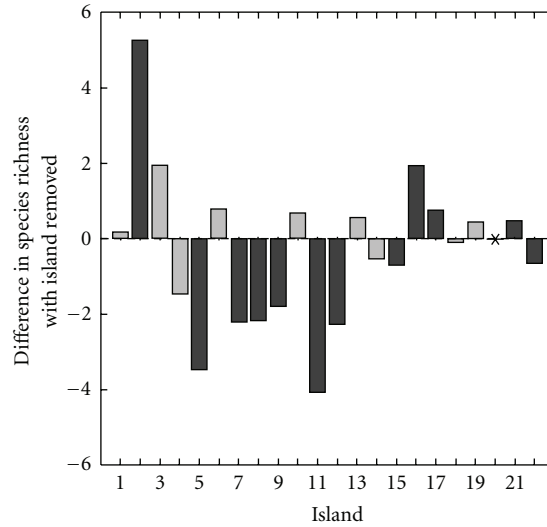
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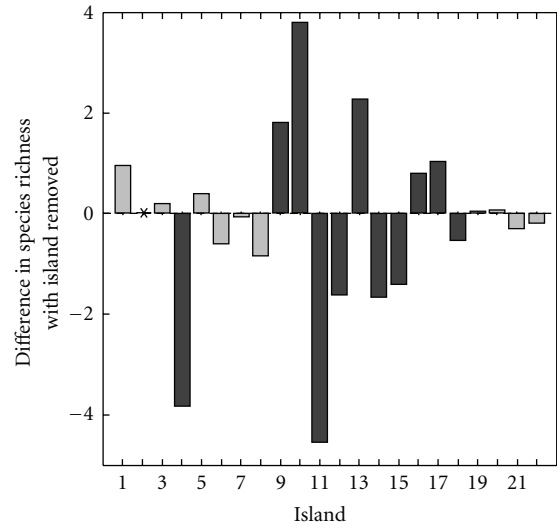
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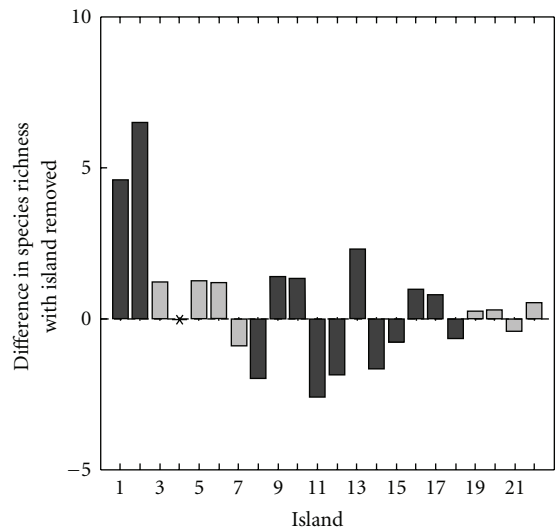
(c)

(d)

(e)

(f)

FIGURE 4: Continued.

(g)

FIGURE 4: Changes in native plant species richness when islands are removed from the archipelago. Islands removed were (a) Isabela, (b) Santa Cruz, (c) Santiago, (d) San Cristobal, (e) Pinta, (f) Daphne, and (g) Tortuga. Darkly shaded bars are differences greater than one standard error of zero. Islands numbers are (1) Isabela, (2) Santa Cruz, (3) Fernandina, (4) Santiago, (5) San Cristobal, (6) Floreana, (7) Marchena, (8) Pinta, (9) Española, (10) Balta, (11) Santa Fé, (12) Pinzón, (13) Genovesa, (14) Rábida, (15) Wolf, (16) Darwin, (17) Seymore, (18) Daphne, (19) Bartolomé, (20) Tortuga, (21) Gardner-Floreana, and (22) Gardner-Española.

partitioned niche space without regard to which niches may be at higher elevations and support fewer species [64, 84]. In contrast to an overestimate on Isabela, Santa Cruz Island was modeled to have 349 species, but in reality there are 409 native plants [69]. The non-lava area of Santa Cruz is only 16% of the nonlava area of Isabela ($358 \, km^2$ versus $2195 \, km^2$), and the maximum elevation on Santa Cruz is almost half that of Isabela (909 m versus 1704 m), but Santa Cruz has almost as many plant species (409 versus 428). The central location of Santa Cruz in the archipelago leads to more species dispersing to that island than others, and that relationship is captured in the agent-based model. Of the 18,640 Galápagos human residents in 2001, most (11,388) lived on Santa Cruz [85]. Perhaps humans have established a greater diversity of native plants on Santa Cruz than would be expected from its geography, transporting species from other islands and nurturing their establishment on Santa Cruz (e.g., [66, 80]).

The techniques I used were effective in evolving species richness similar to observed richness on the Galápagos Islands, but the methods I used were not intended to emulate reality or to duplicate speciation pathways [86]. I used a single colonization of plants from outside the archipelago, but there have been many introductions into the islands [70, 87]. Cross-pollination was simulated here, to speed evolution, but most plants in the Galápagos are self-pollinators [80]. Niche dimensions of the actual vegetation of the Galápagos could be referenced when assigning initial niches to species, or post-hoc comparisons of niches of evolved species may be compared to those of observed species. The geographic distribution of evolved species may be compared to observed distributions, to compare interisland floristic similarities.

The parameters used (Table 1) may be estimated empirically based on Galápagos vegetation. Niche dimensions may be represented using more advanced methods, such as those used in ecological niche factor analysis [27, 29]. Such approaches would be worthwhile, but were beyond the scope of this modest effort. I also do not seek to elevate in importance a single pathway of speciation above others; the plasticity of plants to diversify in reality is unlikely to be on-par with the modeled plant agents and is taxon specific.

The methods I have used may be altered to address other issues or to create neutral models to which observed data may be compared. Each of the examples I cite below has its defenders and critics, and a broad literature base that is not cited for brevity. I include them to suggest pathways of exploration or even refutation, not to condone any view of their importance in biogeography.

5.1. Island Biogeography. The agent-based approach is inherently flexible. In the context of an archipelago, for example, one may easily modify the distance between islands, their areas, elevations or topographies, number, and configuration. The analyses reported here are examples of such a modification.

5.2. Evolutionary Branching and Cladistics. In this agent-based representation of evolving species, the lineage of any individual is fully known. In addition, the area occupied by any species at any stage may be mapped and quantified. These attributes may be used to create a phylogenetic tree for a simulation, or relatedness and distribution may be merged to create area cladograms for any period (or all periods) in a simulation. Modeling agents with evolving niches should

help strengthen the linkage between ecology and historical biogeography (e.g., [12]), as Wiens and Donoghue [88] encourage.

5.3. Taxon Cycle. The ability to create area cladograms for each species in an assemblage throughout a simulation should be useful in studying the taxon cycle [89–91]. Here the surfaces used to define niches (slope, elevation, and lava) were constant, but these may change, for instance to reflect island formation, erosion, or shifts in biomes. A niche dimension may be prey size or body mass, thereby allowing for the evolution of smaller insular body masses.

5.4. Fundamental Versus Realized Niches. In the model, fundamental niches are defined explicitly, or through species packing as evolution proceeds. Each species also has a realized niche represented by the landscape cells it occupies. Both attributes may be output from a simulation and compared quantitatively.

5.5. Order of Colonization. This application used a single colonizing event, with the location of the colonizer randomly located. Colonizers with predetermined niche dimensions may be added to a community in a fully factorial manner to quantify the importance of colonizing sequence in defining the final outcome of island assemblages [2].

5.6. Community Structure. A variant of the method, where *n* species are initialized on the landscape rather than starting with a single colonizing species, will yield communities where the strengths of species interrelationships are adjustable. Systems initialized using randomly assigned niche dimensions may represent disturbed communities colonized by whatever dispersers reach the area. After simulating many generations, species packing as niches evolve may represent long-established communities.

5.7. Invasive Species. A species may be added to an established community that has niche dimensions or other attributes common for an invasive species (e.g., generalist, high seed production [82]). Alternatively, the assumption of a niche dimension defined by a unit normal curve may be relaxed. A normal curve with area slightly greater than unity would be a supercompetitor and potentially occupy large areas of a landscape.

5.8. Neutral Versus Niche Paradigms. The example reported here combines both the niche-assembly and dispersal-assembly perspectives Hubbell [92] discussed. When islands are fully populated by plants, they take-on the quality of a zero-sum game, such that increases in abundance of any one species imply decreases in another [92 : 55]. Species abundances are fully known in simulations, and may be tallied at any time step, to compare their frequency and abundance histograms to theoretical expectations (e.g., zero-sum multinomial, lognormal). In general, in the application here, species share the same properties (e.g., dispersal ability, seed production, maximum age, mutation rates), except their

spatial locations and the niches they evolved, and so are neutral in many attributes.

5.9. Climate Change. The method may be used to estimate declines in biodiversity on island archipelagos under sea-level rise associated with climate change [93, 94] (the topography of the Galápagos Islands means that a sea-level rise of <1 m will not significantly decrease island area or niche diversity). In alpine areas that shrink due to warmer temperatures [95–97], changes in biodiversity may be estimated. More generally, if climatic surfaces are used as components of niche dimensions, those may be changed as the simulation of generations proceeds, simulating shifts in species ranges under climate change.

To reiterate, the modest scope of this effort prevented parameterizing the simulation to represent specific niches of Galápagos plants, or represent evolution of plants in a literal sense. As such, the simulations are not intended to mimic true evolutionary histories in the archipelago. Here, elevation and slope are serving as gross-level surrogates for differences in attributes like precipitation, soil moisture, and temperature, which have not been mapped at the detail I required. However, I see the outcome as more than a 'toy' model, which are sometimes (and sometimes wrongly) disparaged. Instead, the approach uses information that is at greater detail than is traditional in island biogeography analyses. In those analyses, habitat complexity and numbers of niches are simply represented by island area, and sometimes by the maximum elevation of islands [13–17]. Here, topographic differences are used to represent the numbers of niches more completely, and observed patterns of species richness are evolved.

Acknowledgments

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