

Rational landscape decision-making and the SLOSS debate: how can neutral theory help?

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Abstract

Biodiversity is an essential element to a sustainable ecosystem. According to the early literature in island biogeography, large reserves have more advantages in preserving biodiversity than small ones. The debate of Single Large or Several Small (SLOSS) was hence born. No researchers have used neutral theory to examine SLOSS through computational methods before. This study follows a quantitative methodology and evaluates the stochasticity of individual dynamics through simulations in R. Its results suggest that small reserves are preferred in slowing down the extinction rate, and a bridge with high probability strength tends to lead to a quicker homogenisation between islands.

1. Introduction

Biodiversity is an essential element of a sustainable ecosystem. Researchers devote their lives to minimise species extinction through reserve management practices, but whether one big reserve or several small reserves is better in this matter? SLOSS—Single Large or Several Small—is a long-standing debate among ecologists and biologists, of which the answer remains unclear (Tjørve 2010). It started in 1975 when Diamond published the six principles of nature reserve design, which suggest that the size of a reserve has a negative correlation with its species extinction rate (Diamond 1975). Diamond’s work has been cited many times and profoundly influence the modern reserve design practice. Numerous studies have been conducted ever since. While some researchers have strengthened the favouritism in large reserves, a recent study shows that small reserves are the better approach to save species in most empirical studies (Fahrig 2019). Out of 75 academic comparisons regarding SLOSS, Fahrig (2019) claims that only 10% could find evidence in supporting SL. Zhou and Wang (2005) also argue that reserve size may be less a deciding factor of community diversity if the Allee effect is in place, which refers to the phenomenon that one or more species face breeding difficulty due to a small population. Therefore, they propose that “medium-sized” reserves may have the best trade-off balance in reducing species extinction rate (Zhou and Wang 2005). Looking back, one common attribute of these studies is that researchers tended to focus on species solely. Yet, one crucial gap is still missing.

Hubbell (2001) introduced the unified neutral theory two decades ago. Similar to Diamond (1975), it is a concept initially from the island biogeography of MacArthur and Wilson (1967).

The unified neutral theory promotes a biodiversity parameter θ as the sole indicator of the species abundance distribution by assessing individual dynamics within a given habitat area (He and Hu 2005). Hubbell (2001) insists that stochasticity plays an immense role in the demographic of any natural communities; it is a conflicting theory against Darwin’s Theory of Evolution. Surprisingly, regardless of the somewhat naive sounding of the unified neutral theory, it manages to predict various real-world species dispersion that do not make sense under the niche-assembly belief (Matthews and Whittaker 2014). Hankin (2007) computes a series of simulated paths of a dataset that contains 8,419 individuals and 176 species to estimate θ . He finds the results are highly similar to the actual observations. He also advises θ has a positive relationship with the size of a local community, which in a way aligns with Diamond (1975).

Nevertheless, Rosindell, Hubbell, and Etienne (2011) reveals that the empirical application of Hubbell’s work is still limited after a decade since it first published. One potential field would be landscape decision-making and reserve design. Rosindell, Hubbell, and Etienne (2011) point out that the unified neutral theory has made accurate implications on habitat loss with different reserve configurations. Could it be part of the SLOSS debate solution? We have no answers to this question yet, as no researchers have investigated SLOSS using the unified neutral theory before. It is under such background that this research project is initiated.

Consider a nature reserve that is consisted of two connected islands. What would happen if the connection strength was modified or removed? Throughout this study, the unified neutral theory will be applied onto the SLOSS debate, and the relationship between these two reflective academic works will be examined. It is worth noting that one of the six principles that Diamond (1975) proposed has a parallel concept to this study. However, the unified neutral theory is a later publication and was not considered in Diamond’s work. The research utilises the R package of Hankin (2007) and demonstrate how the unified neutral theory can make up some of the missing parts of the current studies in SLOSS and vice versa.

This research is a correlational and experimental quantitative study. Literature reviews and statistical models are used to evaluate the research questions. The methodology, findings and limitations of the study will be discussed sequentially in the following sections.

2. Literature Review

2.1 SLOSS Debate - finding the optimal size of nature reserves

Over the last forty years, there are countless debates regarding whether a single large (SL) or several small (SS) reserves are more beneficial for minimising species extinction. As Tjørve (2010) reveals, all of these can be traced back to 1975 when Jared Diamond first introduces the set of six reserve design principles. Diamond (1975) points out that natural habitats are experiencing change and forced to be fragmented due to human interference. It is crucial to associate area size with species survival rate when it comes to reserve design practice, based on the equilibrium theory. According to MacArthur and Wilson (1967), an island will reach an ideal equilibrium if the immigration rate of new species is the same as the extinction rate of the locals; the equilibrium level is often affected by how isolated the island is and its size.

Diamond (1975) tested the latter factor by studying bird communities resid in different New Guinean rain forests using the species-area relationship formula $S = S_0A^z$. She found that for two of the closest forests to Australia, the one with larger habitat areas retains more species as it is more likely to get hold of the immigrant dispersion. Following this conclusion, Diamond (1975) examines the species-area relationship in a mathematical approach and derives the nature reserve design principles.

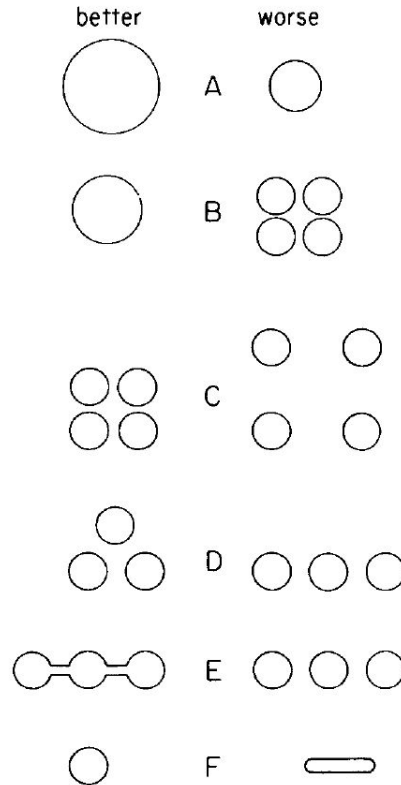


Figure 1: Diamond’s six nature reserve design principles is the beginning of the SLOSS debate

Figure 1 explicitly illustrates the six tactics to design a reserve to maximise biodiversity in a given area. A and B address the first half of the SLOSS debate: a single large reserve is better. Then, principle C shows that if the reserves are equally big, the circle-shaped one will hold a higher equilibrium over the oval-shaped one. When fragmentation is inevitable, Diamond (1975) suggests that the protected areas should be proximate and connected rather than sparse and distanced (D & E). The implementation of buffer zones should also be considered (F). While Diamond’s work provides a foundation of the landscape decision-making process, his favouritism in large reserves does not help tackle the growing infraction of habitats worldwide. In addition, do the six principles developed in 1975 still hold as time goes on? Researchers began to search for answers to such questions.

Burkey (1989) explores SLOSS by simulating the fragmentation effect while considering the stochasticity of island migrants. He demonstrates that the species extinction rate increases exponentially as the reserve area decreases; nevertheless, such species-area relationship

eventually reaches a sigmoidal status as the time span gets infinitely vast. This finding overturns Diamond’s suggestion on pursuing large reserves. Burkey (1989) points out that Diamond’s assumption on extinction rate minimisation equal to biodiversity maximisation may be over-simplified. Similarly, Zhou and Wang (2005) study the metapopulation dynamics and seek to identify an optimal size of habitat area based on the Allee effect. Their research simulates a homogeneous patch network with different numbers of identical reserves. It shows that the Allee effect has a more substantial influence on species extinction than the size of the protected area. Consequently, they form the concept of “medium-sized reserves” and indicate that moderate fragmentation may stimulate a species to survive longer in a local metacommunity (Zhou and Wang 2005).

In recent time, Fahrig (2019) analyses 58 empirical literature related to the SLOSS debate and concludes that SS is predominately more evident in increasing biodiversity. After filtering out the studies that may contain sampling bias towards SS>SL, only 10.6% of the 75 comparisons favour SL; the remainders are either supporting SS (52%) or cannot reach a definite conclusion (22%). The samples papers involve different taxonomic groups from butterflies to exotic plants, and various habitat types such as wetland and urban area. Most of these sub-categories produce a consistent SS>SL ratio (*Figure 2*). Moreover, Fahrig (2019) investigates the reasons why SS>SL is dominating the empirical findings. Individuals of species are more likely to be “rescued” from habitat loss and immigrant to a new area due to the matrix proximity of small patches. He also comments that Diamond’s assumption of all sizes of habitats being equally homogeneous is inadequate to predict SL>SS. Overall, Fahrig (2019) offers an up-to-date and holistic view of the SLOSS debate development in the last few decades. It is also interesting to see how researchers tend to focus on species rather than individuals.

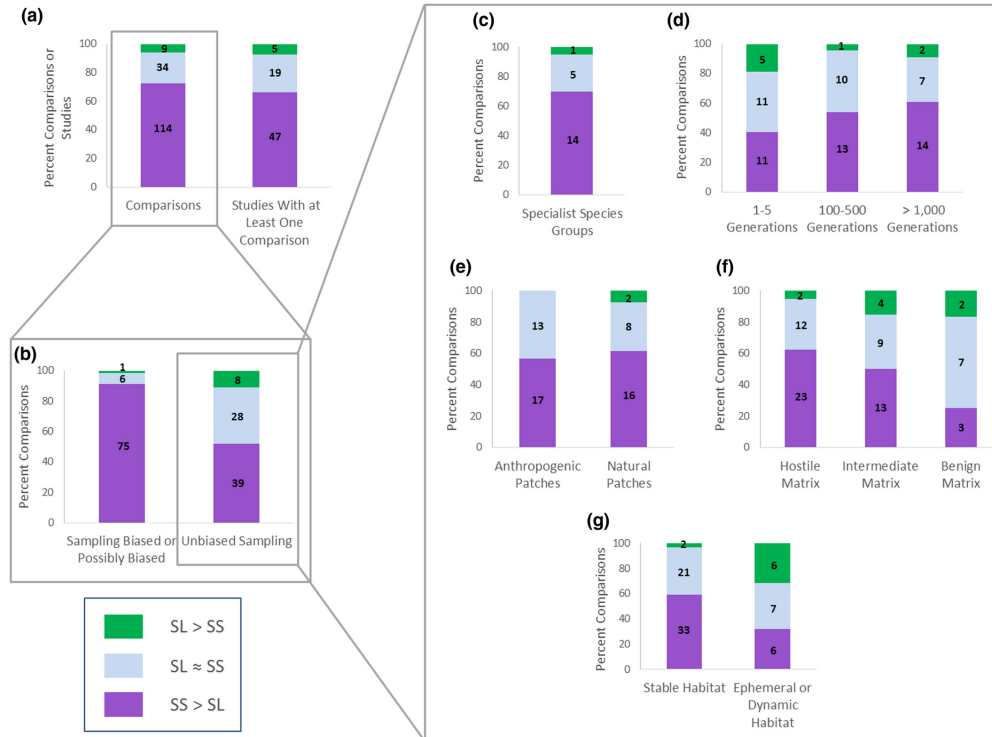


Figure 2: Fahrig compares an abundant amount of SLOSS literature and found the $SS > SL$ is predominant in empirical studies, even after removing the bias favouring SS due to small sample size

2.2 The unified neutral theory of biodiversity

The unified neutral theory is built on the equilibrium theory of MacArthur and Wilson (1967) and brings novel perspectives to the matter of relative species abundance at the time. It suggests that the birth rates and death rates are equal among individuals within a local community, which means the change of biodiversity over different periodic lengths of generations is entirely due to random chance of disturbance (Hubbell 2001). To prove this, Hubbell (2001) develops a simple dynamics model to simulate the effect of zero-sum ecological drift of a local community (*Figure 3*). The model's parameters include the community size J , the immigration rate m and the abundance of the species at the beginning of each disturbance cycle. Despite the simplicity of the model, it successfully measures the biodiversity within a metacommunity that could not logically explain under the niche-assembly theory. That is, “the simultaneous existence of both abundant and rare species” (Hankin 2007).

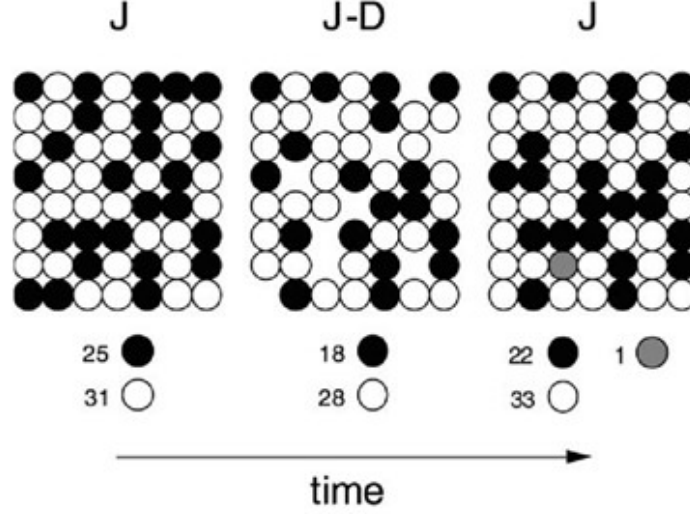


Figure 3: The zero-sum ecological drift model under the unified neutral theory of biodiversity

Hubbell (2001) clarifies the unified neutral theory model under two scenarios regarding the final biodiversity status of the simulated community. One is called the absorbing case; the probability of having mutants is zero. It means that the island will eventually become monodominant, and the probability density function is U-shaped in terms of the species relative abundance. On the other hand, he explains that if the island is open to immigration, the local species will likely go extinct and re-enter the same area as an outsider. The species relative abundance, in this case, will be mirroring the metacommunity. Moreover, the model reveals that the larger a community is, the longer it will take for any given species on the island to go extinct after controlling the disturbance rate (Hubbell 2001).

Matthews and Whittaker (2014) claim that the profoundness of Hubbell's theory is not just about neutrality; it not only considers the stochasticity of genetic drift like the previous neutral theory but also treats dispersion as a crucial factor of the community dynamics. The unified neutral theory is dispersal-assembled (Hubbell 2001). As a provoking voice in the academic arena of species and evolution, the unified neutral theory encounters a few difficulties, as Rosindell, Hubbell, and Etienne (2011) recall. They review the application of the unified neutral theory after the first decade of its publication and find that it has not progressed much. The most extensive use is to predict species abundance in sample communities, yet its future applications are promising as it is slowly drawing the attention of researchers around the world (Rosindell, Hubbell, and Etienne 2011). Phylogenies is one of the domains that the unified neutral theory can be of help, with methods such as Approximate Bayesian to estimate phylogenetic patterns. Rosindell, Hubbell, and Etienne (2011) also think that the unified neutral theory is tremendously valuable for conservation. Several papers used it to evaluate habitat loss and fragmentation, and the results are significant.

Hankin (2007) develops a software package in R to demonstrate the unified neutral theory in a computational manner. One example illustrates excellent goodness of fit regarding the species rank in abundance between the actual data and the prediction of unified neutral

theory, supporting the practicality of Hubbell’s work is beyond mathematical assumptions (*Figure 4*). Hankin (2007) also simulates the maximum likelihood estimates of biodiversity parameter θ across three different sizes of local communities. The result finds the more prominent communities have a higher m and θ , but the gap is getting closer as the community size increases.

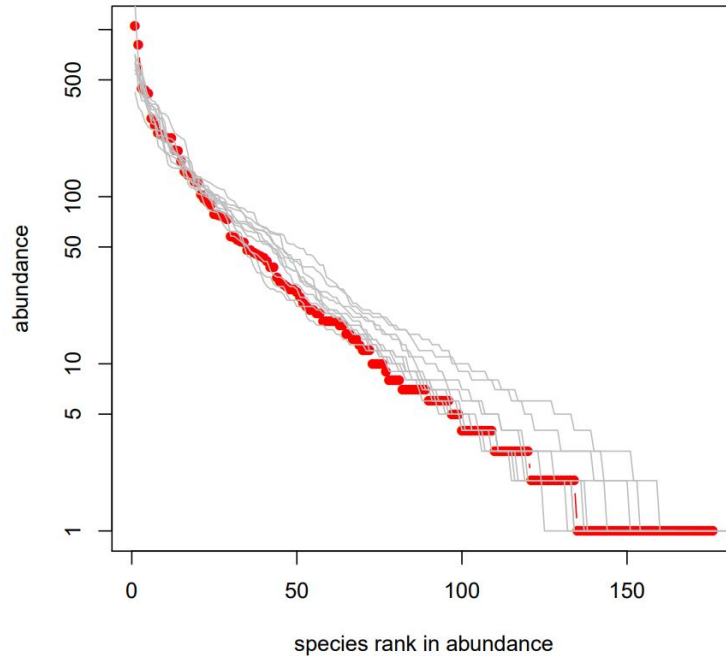


Figure 4: The `untb` package in R written by Hankin helps researchers associate the unified neutral theory with empirical data. This figure is an example of comparing the “saunders” dataset to a randomly generated curve with function `rand.neutral()`

3. Research Design

This research is a quantitative study in the field of biodiversity and mathematics. According to Bloomfield and Fisher (2019), a quantitative methodology is a research approach that aims to find the one true answer to a question via numerical and objective evidence. There are four types of quantitative research design: descriptive, correlational, quasi-experimental and experimental. Correlational research investigates the nature of a relationship between two or more variables, whereas experimental research explores the hidden connections between them (Bloomfield and Fisher 2019). Since this study explores how neutral theory can address the SLOSS debate and contribute to the landscape decision-making process, its foundation is correlational and experimental.

Three main questions were examined in this study:

- To what extent does the connection size affect the biodiversity status of the two islands?
- How soon can these two islands lose half of the total biodiversity?
- How long can these two islands retain 75% of the total biodiversity?

3.1 Methodology

The study followed a step-wise strategic process with four main actions: research question, literature review, statistical modelling and findings and discussion. See *Figure 5* for a graphical explanation.

The first step is to conduct an adequate amount of literature reviews regarding the unified neutral theory and the SLOSS debate. The papers this research surveyed range from 1975, right from the beginning of the SLOSS debate, to 2019, providing up-to-date critiques and perspectives to the relevant matters.

Next, a feasible reserve prototype was identified for the statistical model. Recall the six design principles of Diamond (1975); principle E describes that when fragmentation is non-avoidable, connecting the habitats is better than isolating them. However, he did not address the details of the connection methods, such as how large the joining surface should be and how exactly that would change the biodiversity status across all related reserves. Thus, this research constructed an algorithm to mimic the biodiversity status of two adjacent and identical islands. For demonstration purpose, they are named *Rangtito* and *Motutapu* as a tribute to the city the researcher lives in, Auckland.

Then, simulations were performed on different community size and bridge strength configurations, following the algorithm rules. Explanations of model outputs and sample paths are demonstrated throughout the whole study. **The count of species and the Bray Curtis Dissimilarity** are used to assess the research proposed questions. The dissimilarity between habitats, as Baselga (2013) states, is an essential parameter when evaluating a local community's biodiversity patterns. The Bray Curtis is one of the most commonly used equations to derive the dissimilarity probability; hence it is chosen as a secondary measure for this research. The species count was the primary measure.

The Bray Curtis Dissimilarity equation is displayed below:

$$BC_{ij} = 1 - \frac{2 * C_{ij}}{S_i + S_j}$$

Finally, the important findings and limitations of this study were discussed.

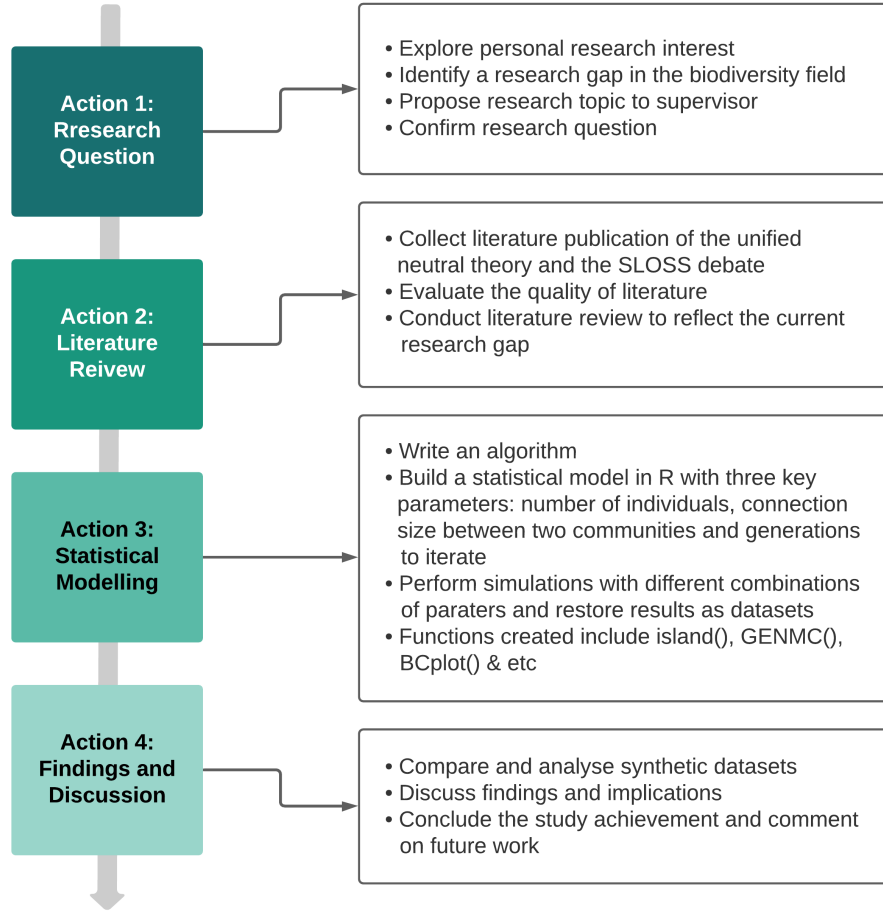


Figure 5: The strategic process of this research

3.2 Algorithm

Create a metacommunity J_m with ten singletons of species. Each individual will be randomly assigned to one of the two islands. A bridge p is connecting the islands with the probability between 0 to 1. When $p = 0$, the two islands are isolated from each other; when $p = 1$, they are assumed to function like one big reserve. According to Hubbell (2001), when an individual dies from a site, their spot will randomly be filled by another individual.

1. Consider a time step sufficiently short for only a single individual to die
2. Choose a site at random on either island; the individual at this site dies
3. With probability $1 - ((J - 1)^{-1} * \frac{J}{2} * p)$, an individual of species chosen at random from the same island is born
4. With probability $((J - 1)^{-1} * \frac{J}{2} * p)$, an individual of species chosen at random from the counter island is born
5. p refers to the size of the bridge with a probability between 0 and 1
6. The probability of mutants is set to 0 intentionally

The algorithm is a modified work of Hankin (2007).

3.3 Data acquisition

This study used artificial data generated in R to simulate the biodiversity change of two imaginary islands. No primary data was required and collected. The data acquisition is part of the statistical model built. After testing the model with different parameters, the results were saved into datasets for analysis purpose.

3.4 Statistical modelling in R

This section introduces several R functions the researcher has written to facilitate the analysis process of the study. The community created for demonstrations has six individuals (sites) with a bridge sized 0.5 unless otherwise specified.

3.4.1 island()

A sample path generator that wraps the algorithm from *Section 3.2* into one command. It includes three parameters: **n** (number of individuals), **b** (the size of the bridge) and **g** (generations/time steps to iterate). An empty data frame named “rm_step” is constructed to store the change of diversity dynamics at each generation.

The R codes below generate a synthetic dataset generated using island(). Column 1 indicates the order of generations within the simulation; column 1-3 are individuals “live” on *Rangitoto* and column 4-6 are the ones on *Motutapu*; column 7-8 are the counts of species on the islands; the final column is the Bray Curtis Dissimilarity Index calculated using the count information.

Verify that at gen0, each island has three singletons, and none of the species is overlapped. The species abundance at generation one is minimal.

```
island(n=6,b=0.5,g=10)
```

```
##      rangi rangi rangi motu motu motu species_count rangi_count motu_count
## gen0    J5    J6    J3    J1    J2    J4           6           3           3
## gen1    J3    J6    J3    J1    J2    J4           5           2           3
## gen2    J3    J6    J4    J1    J2    J4           5           3           3
## gen3    J3    J6    J4    J1    J2    J4           5           3           3
## gen4    J3    J6    J4    J1    J2    J3           5           3           3
## gen5    J3    J6    J4    J1    J3    J3           4           3           2
## gen6    J3    J4    J4    J1    J3    J3           3           2           2
## gen7    J3    J4    J4    J1    J3    J3           3           2           2
## gen8    J4    J4    J4    J1    J3    J3           3           1           2
## gen9    J4    J4    J4    J1    J3    J4           3           1           3
## gen10   J4    J4    J4    J1    J4    J4           2           1           2
##      BrayCurtis
## gen0      1.00
## gen1      1.00
## gen2      0.67
```

## gen3	0.67
## gen4	0.67
## gen5	0.67
## gen6	0.67
## gen7	0.67
## gen8	1.00
## gen9	0.67
## gen10	0.33

Figure 6 visualises a sample path with changes at each step of both islands. There are ten sites in this community. When the bridge size is 0.5, a 72% chance an individual from the same island will replace the empty site; the remaining 27% go to the counter island. The weighted probability is due to the imaginary distance between islands and only relevant to individuals instead of species. In the beginning, three sites were filled by individuals from the same island; the first “mutant” appeared at step 4, and once they “immigrated” to the counter island, they tended to stay (J9 as an example). Since the simulation was initialised with all singletons, the biodiversity of these two islands started to decrease from generation 1. Same for the speed to reach monoculture. The sample path shows no biodiversity change from generation 35 (it remains to have three species until generation 50).

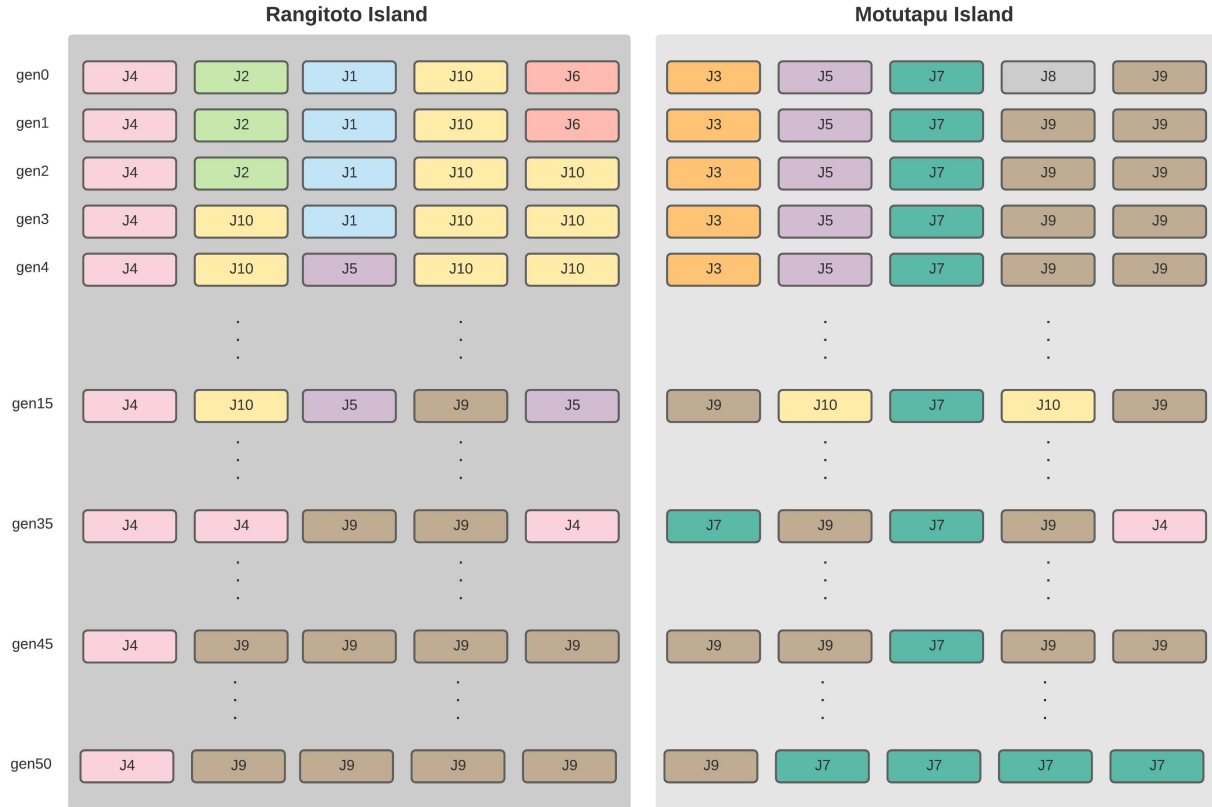


Figure 6: A sample path of the biodiversity changes of two islands with $n=10$, $\text{bridge}=0.5$ and $\text{gen_n}=50$. J10 was the first species that became abundant and crossed the island. At generation 15, J9 started to spread, and it slowly replaced all the individuals of J10. Despite that there was mainly one individual of J7 in the last 45 time steps, this species began to take over at the 50th generation.

3.4.2 `bio_max()`, `bio_min()`

`bio_max()` calculates how long a given community can retain a certain level of diversity by outputting the corresponding generation. It has three parameters: **df**, **column** and **number**. **df** is any datasets that are generated using `island()`; “column” specifies the evaluation method to use (either “speciec_count” or “BrayCurtis”); the last one is the targeted biodiversity level (for species count, it is going to be a whole number, for BC Dissimilarity, it will be a probability between 0 to 1.)

```
# Check the longest generation that this community can retain 75% diversity
df <- island(6,0.5,20)
rownames(bio_max(df,"species_count",6*0.75))
```

```
## [1] "gen6"
```

In contrast, **`bio_min()`** calculates how soon a given community can reach a certain level of

diversity. It helps find out the quickest speed to arrive at the monocultural status.

3.4.3 BCMC(), SPECMC(), GENMC()

BCMC stands for Bray Curtis Monte Carlo. As suggested by its name, this function runs Monte Carlo simulations on a given community configuration. **n**, **b**, **g** are used to design the community and the length of each sample path; **t** specifies simulation times. SPECMC() is a similar command but calculates the actual number of species instead of the dissimilarity index. Finally, GENMC() iterates the bio_max() and bio_min() functions to obtain a frequency count of generations at a given biodiversity level. *Table 1* demonstrates the first ten rows of five sample paths simulated with the BCMC() function.

Table 1: Monte Carlo Simulation of the Bray Curtis Dissimilarity

path1	path2	path3	path4	path5
1.00	1.00	1.00	1	1.00
1.00	1.00	1.00	1	1.00
1.00	0.67	0.67	1	0.67
0.67	0.33	0.67	1	0.67
0.67	0.33	1.00	1	0.67
0.67	0.67	0.67	1	0.67
0.67	0.33	0.67	1	0.67
0.67	0.67	0.33	1	0.67
0.67	1.00	0.00	1	0.67
0.67	1.00	0.33	1	0.67
0.67	1.00	0.33	1	0.67

3.4.4 BCplot(), drawplot()

Two plot functions are also created to illustrate the change of measurement over time. The demonstration of them can refer to the analysis below.

More information regarding the algorithm and R functions this research used can be found on GitHub: www.github.com/lillianlu-nz/stem

4. Application and Findings

4.1 Implication of “bridge”

When having a single large reserve is impossible, Diamond (1975) claims that one practical approach to reducing species extinction is to connect all the small ones nearby. Here, functions

from *Section 3* are applied to analyse the implication of a bridge on the individual dynamics between two identical islands, with a changing size from 0 to 1 (step length 0.1).

4.1.1 Species abundance

The research first analysed the expected number of species count of four different sizes of communities after they experience ten turnover times. That is the 100_{th} generation of a $J_m = 10$, the 500_{th} generation of a $J_m = 50$, and so forth. *Table 2* shows the output of 100 simulations at each bridge strength. Surprisingly, **changing the probability strength of the bridge does not seem to affect the predicted species count**. The numbers shift up and down with no more than one unit among the four communities. The only time there is a notable difference is when $b = 0$; the minimum species count would always be two if the islands are isolated. The research noticed that the larger communities indeed have a higher species count; more investigations will follow. Also, even with the smallest community, ten cycles of site replacements are not long enough to reach monoculture.

Table 2: Expected Species Count After Ten Turnovers

n	b0	b0.1	b0.2	b0.3	b0.4	b0.5	b0.6	b0.7	b0.8	b0.9	b1
10	2.06	1.70	1.44	1.46	1.40	1.39	1.39	1.33	1.38	1.29	1.24
50	5.28	4.98	5.03	5.02	4.94	5.02	4.93	5.17	5.03	5.05	4.70
100	9.79	9.41	9.51	9.64	9.62	9.40	9.31	9.40	9.68	9.48	9.71
500	46.21	45.62	46.34	46.01	46.31	45.57	45.43	45.45	45.62	45.28	45.25

4.1.2 Island similarity

Next, the same process was repeated to estimate the expected Bray Curtis Dissimilarity (also called the BC Index). This time, **the bridge strength is a significant factor in predicting the index level** (*Table 3*), especially for small communities. Similar to the expected species count, when the community is large, the dissimilarity between two islands tend to last longer. Even though the differences are very subtle between the three larger communities tested ($J_m = 50 - 500$). The results also find that the BC Index all went down by nearly half once the bridge is open ($b > 0$). The only case when the islands can remain 100% dissimilar to each other is when the bridge is closed ($b = 0$).

Table 3: Expected Bray Curtis Dissimilarity After Ten Turnovers

n	b0	b0.1	b0.2	b0.3	b0.4	b0.5	b0.6	b0.7	b0.8	b0.9	b1
10	1	0.50	0.25	0.27	0.14	0.16	0.10	0.09	0.07	0.08	0.06
50	1	0.63	0.46	0.37	0.31	0.27	0.27	0.24	0.20	0.21	0.20
100	1	0.62	0.46	0.39	0.33	0.30	0.27	0.24	0.21	0.22	0.21
500	1	0.64	0.47	0.38	0.33	0.30	0.28	0.24	0.21	0.24	0.22

4.1.3 Regression analysis

We already know the bridge strength has something to do with the BC Index, but does its impact vary with the scale of the community as well? A linear regression analysis was deployed in R to quantify this. The result from *Table 4* proposes that bridge strength is the only factor that has a statistical influence on predicting the BC Index (p-value < 0.0001). Neither the number of individuals or the interaction term are a significant predictor. It is reasonable to say that no matter the size of a community, how the bridge affects the BC index does not change. This explains the finding in *Section 4.1.2* regarding the minimal difference of BC index across the three large communities. The difference observed between $Jm = 5$ and the other communities is not enough to support the SL>SS statement.

Table 4: Linear Regression Analysis

term	df	sumsq	meansq	statistic	p.value
n	1	0.0413975	0.0413975	1.7462867	0.1938532
bridge	1	1.7031854	1.7031854	71.8462120	0.0000000
n:bridge	1	0.0011073	0.0011073	0.0467117	0.8299858
Residuals	40	0.9482395	0.0237060	NA	NA

Finally, *Figure 7* provides a visual demonstration of the bridge effect on species count (left) and the BC index (right). Observing that even though the BC index levels differ by the community size, it is not statistically significant to make any conclusions on the correlation between them.

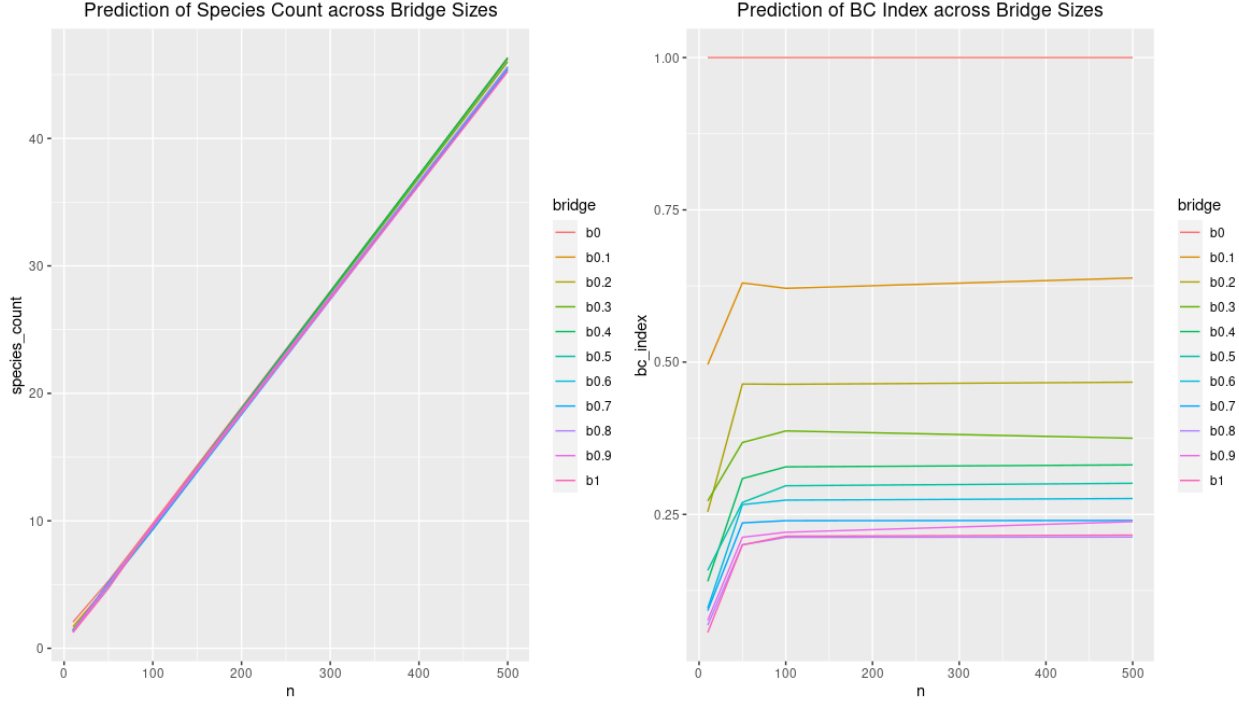


Figure 7: Bridge effect on species count and the BC index

4.2 Species extinction estimation

How long would it take for the islands to lose 50% of the local species? *Figure 9* visualises the change in the numbers of species of four different J_m configurations over 200 timesteps, five sample paths each. The bridge probability strength is set to the maximum. The grey dot lines mark the 10%, 50% and 90% of the corresponding variables, which help provide an intuitive understanding of the change. Thus, it is likely for a community with ten singletons to lose half of the species at around ten timesteps. In contrast, the time for 50% of the species within a large community to go extinct can be very long (bottom right; the species count did not even go under 70%).

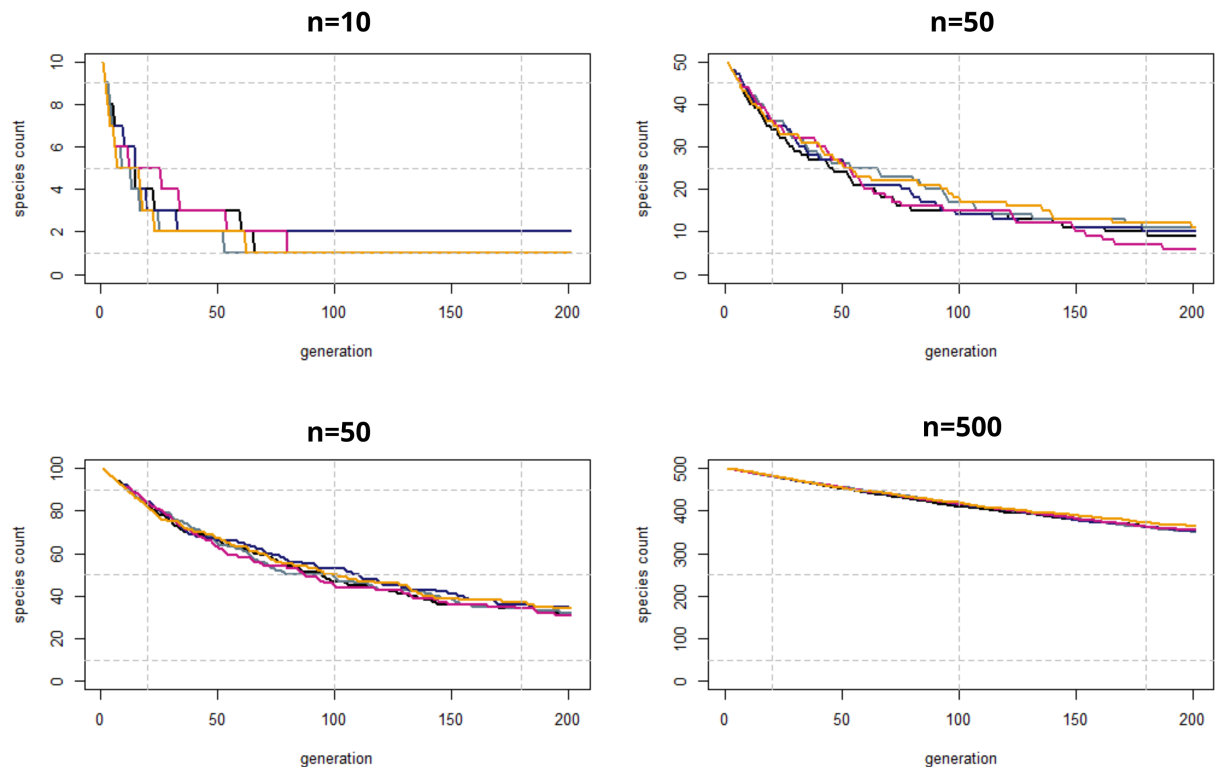


Figure 8: Change in the numbers of species of different local communities

Nevertheless, even though the decrease of species shows a quadratic pattern over time, which aligns with Diamond (1975)’s observation regarding the species-area relationship, such results may look too obvious. 50% species loss for a hundred-individual community means there are 50 species gone; the number became 5000 if the community has 10000 residents initially. **Thus, The research suggests that it would not be a solid argument for choosing SL over SS just because the large communities take a longer time to lose 50% of their species.**

Turnover time, on the other hand, may provide more insightful information to understand the species extinction rate. *Table 5* contains the estimated quickest speed to lose half of the species across different communities, as well as the corresponding turnover time. The results from $n=10$ to $n=500$ are generated from the mode observation of 1000 simulations. The results from $n=1000$ and onward are calculated using the mean of 10 simulations. As expected, “ n ” and “ gen ” has a positively correlated relationship. However, the turnover time for these communities to lose 50% species does not differ much. On average, it takes less than one cycle of time to do so. *Figure 9* reminds us how different conclusions may have been made on the SLOSS debate based on the parameters chosen (timestep vs. turnover time).

Table 5: Estimated Speed of 50% Species Loss

n	bridge	timestep	species_left	turnover_time
10	1	8	5	0.8000000
20	1	18	10	0.9000000
30	1	28	15	0.9333333
40	1	38	20	0.9500000
50	1	44	25	0.8800000
60	1	58	30	0.9666667
70	1	68	35	0.9714286
80	1	86	40	1.0750000
90	1	88	45	0.9777778
100	1	94	50	0.9400000
200	1	199	100	0.9950000
300	1	287	150	0.9566667
400	1	395	200	0.9875000
500	1	505	250	1.0100000
1000	1	1001	500	1.0010000
2000	1	2020	1000	1.0100000
5000	1	4983	2500	0.9966000
10000	1	9987	5000	0.9987000

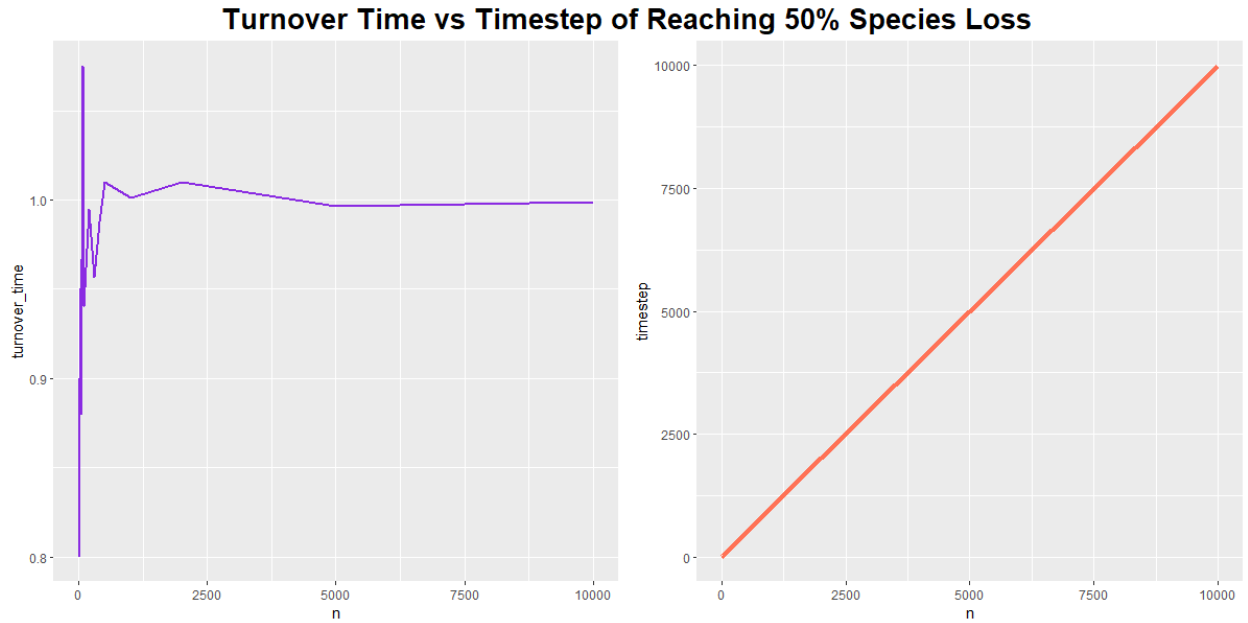


Figure 9: Evaluate the 50% species loss by turnover time (left) and by timestep (right) gives totally different implications. The former suggests that the community size has no effect on predicting species extinction rate while the latter tells the opposite.

At this moment, we know the speed to lose 50% species is one turnover time regardless of the community size; however, in *Section 4.1.1*, the study observed that the percentage of species left after ten turnover times is different. Therefore, another set of simulations are performed to quantify the inference of turnover time. *Figure 10* illustrates the percentage of species loss within ten turnovers, and the red dash line is the 90% mark. Thus, for the small communities (10 and 20 individuals), the species extinction rate is slower than the large ones. As the community size gets bigger, there is not much difference in speed.

Based on this observation, **the research concludes that small reserves are preferred in slowing down extinction rates under the unified neutral theory** while the areas are connected (size does not matter).

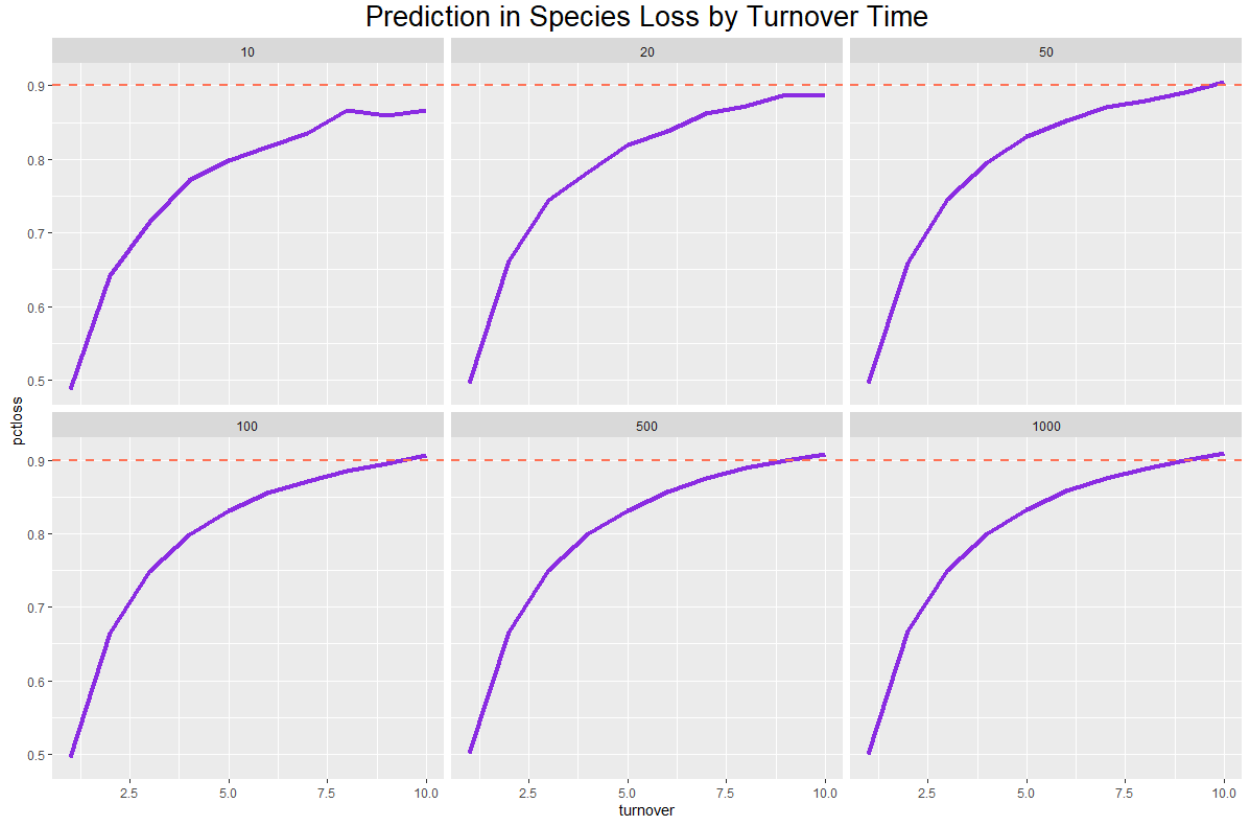


Figure 10: Under the unified neutral theory, small reserves take a longer time to reach 90% species loss than large reserves.

The study also looked into the Bray Curtis Dissimilarity. *Figure 11* shows the turnover time of reaching 50% dissimilarity (equals to 50% similarity) between two islands, broken down by bridge strength. It is clear that **under the unified neutral theory, the larger the bridge is, the quicker two connected habitats will become similar in species**. With $b = 0.1$, ten turnovers are not long enough to reach the 50% threshold; it is also the only configuration that creates a linear line.

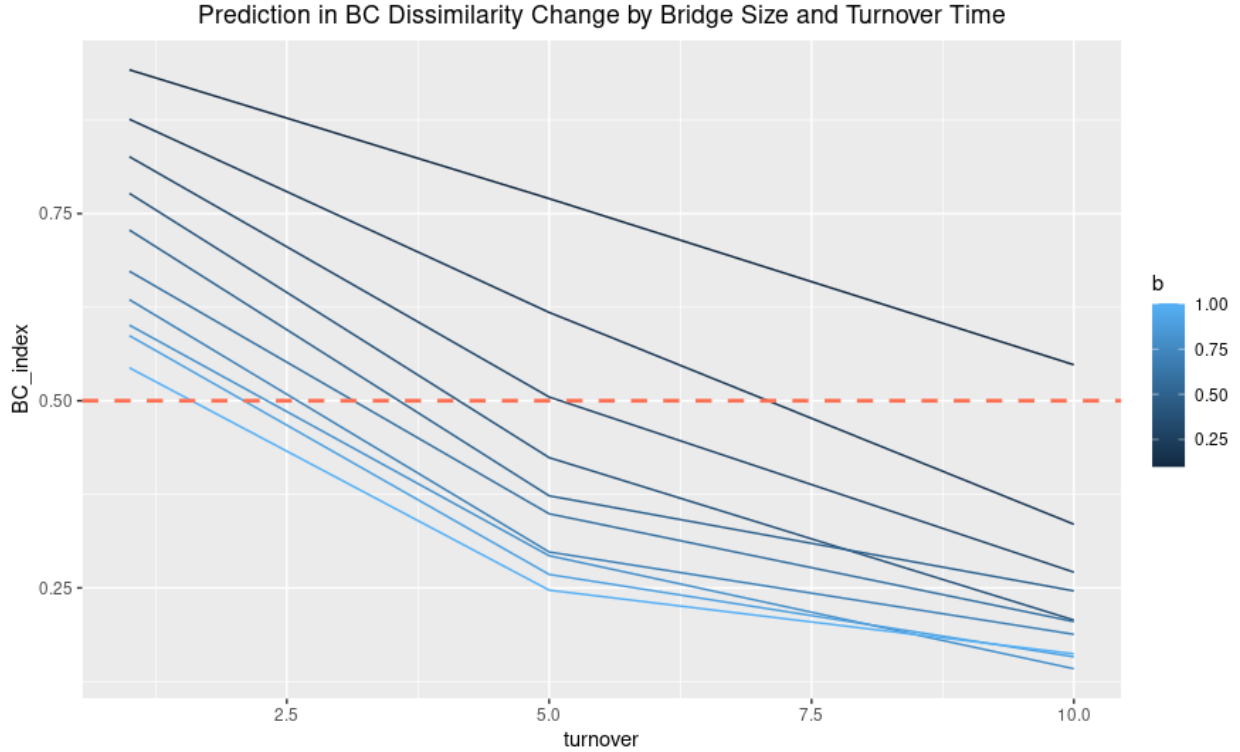


Figure 11: Under the unified neutral theory, larger bridges will lead to quicker homogenisation between reserves.

4.3 Biodiversity retention and SLOSS

One of the drawbacks of Diamond's work, as raised by Burkey (1989), is that he only considered species loss instead of the overall biodiversity status within a given area. Therefore, apart from analysing the species extinction rate, the study also investigated how long a community can keep its diversity at 75% by evaluating the turnover time. We already know the speed for any community size to lose 50% of its local species is around one turnover time, so the researcher took a closer look at between 0.1 to 1 turnover time and identified the average position of maintaining 75% biodiversity. *Figure 12* illustrates the result, and it is evident that these lines look identical. Even though we also observed a linear relationship between biodiversity level and the number of individuals, it is again not strong enough to support the SL argument.

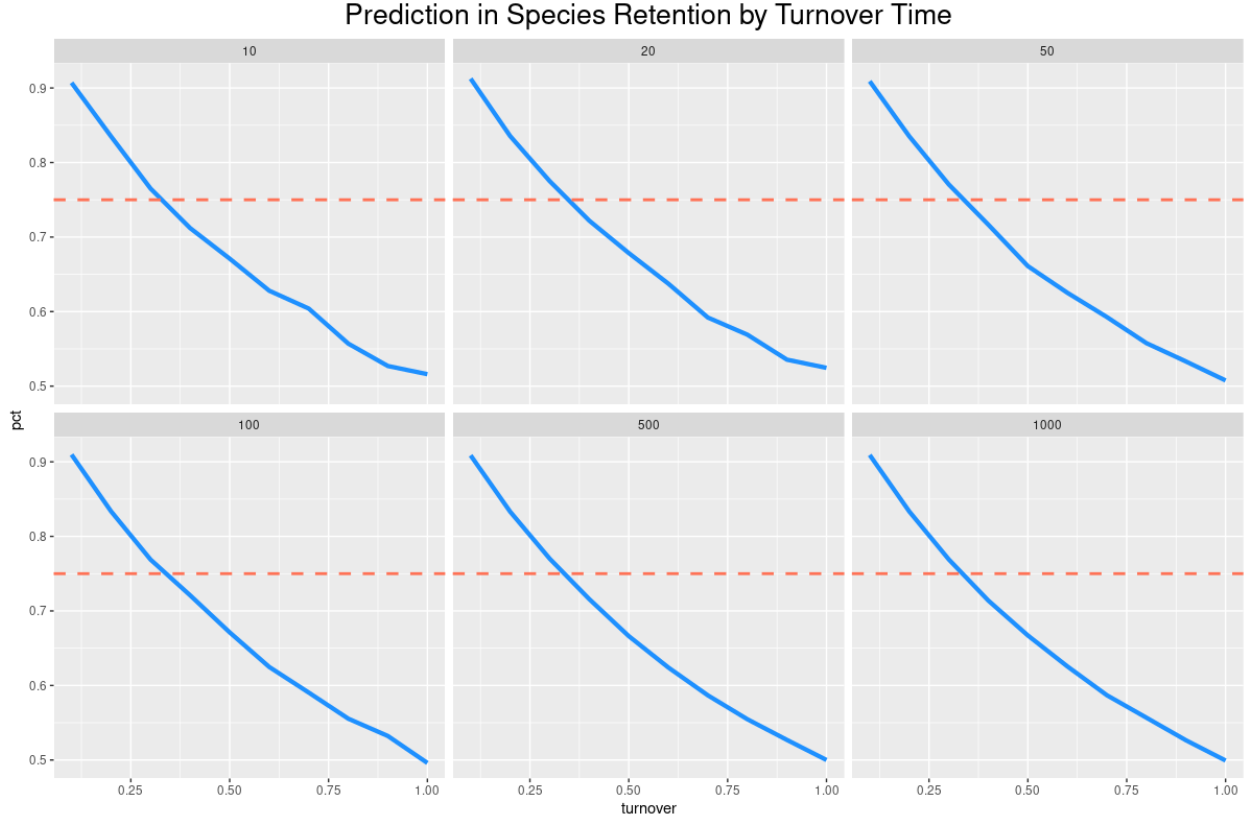


Figure 12: Under the unified neutral theory, there is no proof that the larger reserves can hold a level of biodiversity longer than the small ones.

To confirm the finding, the study computed the change between species by each increment of turnover time and calculated the mean and variance grouped by community size. As displayed in *Table 6*, the variation of change pace is very similar across different community size, supporting that **reserve area has no relation to how long they can retain locally diverse**.

Table 6: Change Statistics of Different Communities

n	mean	variation
10	0.039100	0.0005490
20	0.038800	0.0005288
50	0.040140	0.0004816
100	0.041370	0.0004500
500	0.040870	0.0004532
1000	0.040996	0.0004555

Finally, the study would like to refer back to *Figure 11* and discuss the expected turnover

time of 75% BC Dissimilarity. There are only four lines actually crossed the 0.75 benchmark and they are the bridges that are wider than 0.6 (note that $b=0$ is not showing on the graph). **It is reasonable to believe that when the bridge is smaller than 0.6, the community is expected to at least be 25% similar to the counter island before reaching one turnover cycle.**

5. Conclusions

Through a series of simulations in R, this research finds that the unified neutral theory offers new perspectives to the SLOSS debate. It follows a quantitative methodology to demonstrate the biodiversity variation of two connected islands under the stochastic dynamics of individual births and deaths.

The model assessed the implication of the bridge by tuning its probability strength against different community scales. Only a weak correlation was found regarding the species count when the bridge is closed; in this case the minimum species number of the islands will always be two. Thus, the bridge was set to 1 for the remaining analysis when using species count as the measure, focusing on understanding the link between species extinction rate and community size. Also, both timestep (generation) and turnover time were tested as the rate unit, and the latter is deemed more suitable as it is proportional to the community size. The study discovers that small communities (below 20 individuals) are slower than the larger ones at reaching a 90% extinction of species. Yet this difference is not apparent in communities larger than 50. A similar experiment was performed to test the longest hold-on time of biodiversity, and it concludes that the unified neutral theory gives no indications on this matter.

Replacing the measure from species count to the Bray Curtis Dissimilarity shows a strong correlation with the bridge strength ($p\text{-value} < 0.0001$). A larger bridge means a quicker speed to reach homogenisation between islands under the neutral theory. Also, for bridge strength lower than 0.6, it is sensible to expect the two islands to reach at least 25% similarity before experiencing one turnover.

Overall, this research is a computational juxtaposition to put two biodiversity topics together and evaluate them interchangeably. The association between the SLOSS debate and neutral theory had not been seen before. It introduces a fresh mathematical perspective to the landscape decision-making process, specifically regarding habitat size. It also encourages future researchers to understand and expand the subject matter by utilising the easily replicable simulations in R. All functions written in this study are accessible through the GitHub link in *Section 3*.

6. Limitations and future work

There are some limitations of this study.

First, it would have been decent to compare the results to Fahrig (2019)’s investigations in

those SLOSS studies, yet it is hard to verify whether the simulations reflect the real-world observations. The quantification of the bridge probability strength was also ambiguous.

Second, Hubbell (2001) considers two scenarios when discussing the zero-sum ecological drift in his book. One is when there are no mutants, and the other is when there are mutants with a probability from 0 to 1. This study only evaluated the first scenario, which does not fully justify the unified neutral theory on SLOSS.

There are other avenues to explore within this study. For example, testing different combinations of nature reserves, such as size, number of residents and connection length. Also, the findings in *Section 4* are restricted to the performance of the algorithm. It assumes two identical islands with the simplest design to secure a deliverable outcome. Should more configurations have been considered, a more holistic picture of the research topic may be obtained. There are some limitations of this study.

Acknowledgement

The research process provided a steep but exciting learning curve, which I enjoyed very much. I would like to express my deep gratitude to my research supervisor Robin Hankin, who offered enormous help in biodiversity and statistics along the way. I am continually encouraged by his reminder that “the wall of science is built brick by brick.” I hope my research sheds some insights into the SLOSS debate and the world of biodiversity.

I would also like to thank my classmates Yi Yang and Wenqiang Liu for their willingness to give suggestions and motivational support.

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