Faculty of Science & Technology

Environmental Factors Influence the Genetic Diversity of primates using a hypothesised situation established by an Individual Based Model.

A dissertation submitted as part of the requirement for the BSc (Hons) Ecology and Wildlife Conservation.

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Abstract

Although environmental impacts such as fragmentation and habitat amount on animals have been the main focus of many ecological studies, the effect of these environmental impacts on genetic variation within species is often overlooked. As anthropogenic disturbances such as urban development and over exploitation of habitats gradually increases, these environmental factors become more severe, impacting diversity of both flora and fauna in multiple ecosystems. It is essential to study genetic variation in both fauna and flora in order to understand the full spectrum of impacts (e.g. loss of biodiversity, loss of genetic diversity, isolation, speciation and extinction) which environmental factors hold. Primates as keystone species inhabit highly diverse and dense environments many of which are threatened with ongoing environmental and anthropogenic pressures, this provides a requisite to study genetic diversity in this taxa. The aim of this study is to investigate how genetic diversity in primates is impacted at different scales of environmental effects, to do this, an IBM (Individual-Based model) was created which uses various scales of (1) fragmentation; (2) habitat amount; and (3) dispersal distance. Within the model, (A) population size; (B) allelic richness (used alongside (C) to calculate diversity); and (C) heterozygosity, are recorded to analyse alterations in genetic diversity at different scales of environmental impact. To understand how gene dispersion within different species of primates would be impacted, the same levels of impacts were used on populations with a short (2 year) inter-birth interval (r-selected species) and were compared with populations with a long (5 year) inter-birth interval (K-selected species). It is hypothesised that 1, 2, 3 and A would impact B and C e.g. more extreme environmental pressures and population dynamic changes would reduce the genetic diversity of both r and K-selected species. Results indicate that fragmentation is the best environmental indicator and determinant of genetic diversity, whereas, habitat amount, dispersal distance and population size had little direct impact. Indirect effects between habitat amount, dispersal distance and population size were seen and changes in genetic diversity occurred when these factors persisted together.

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Contents

1.0 Introduction

Changes in genetic variation are caused by multiple factors. Some factors benefit the dispersion of genetics throughout populations and others highly reduce and limit it. Factors which drive genetic variation include; species dispersal ability and distance, life history traits and geographical alterations e.g. isolation and stochastic events (Manel et al 2010). Many environmental factors impact genetic variation between individuals and populations; fragmentation, population size, suitable habitat amount and population density are the major issues (Spielman et al 2004). Variation is important to ensure the fitness of individuals and populations thus securing diversity and survival rates in both species and habitats (Lande and Shannon 1996). The interaction these factors hold on genetic variability is insufficiently understood for primates, this study investigates these interactions and explores changes seen in genetic variation whilst applying this information to primates.

1.1 *Background*

Environmental factors and anthropogenic disturbances are a leading cause of changes in population density of a wide range of animal and plant species over time and current increases in disturbances and climate change are leading to a wide range of extinctions (Ceballos and Ehrlich 2002). One important factor in the risk of extinction is the genetic variability remaining in increasingly fragmented populations. The fewer individuals in smaller populations leads to a higher risk of local extinctions caused by a reduction in gene pool size which often results in the Allee effect (Courchamp et al. 1999). Learning the impact of environmental pressures on population genetics is important for not only the survival of the species but also for biodiversity. Biodiversity increases productivity within ecosystems, giving significance to every individual found there. It is of major importance to maintain and conserve biodiversity as it ensures the survival and sustainability of all species in the ecosystem (Hunter 1999). The most important environmental factors are fragmentation and habitat amount as these are both known to have negative impacts on biodiversity and species abundance.

Fragmented environments reduce biodiversity (Fahrig 2003) leaving habitats in unprotected conditions. The lack of connectivity caused by fragmentation widely impacts both fauna and flora which is known to have serious implications for future generations (Aguliar et al. 2008, Hanski 2005). Species worldwide are negatively affected by fragmentation, some of which are now in vulnerable and extremely threatened states (Cushman 2006, Mace and Lande 1991). It is seen to be problematic for many species

such as various primates including *Gorilla* (gorilla), *Pongo* (orangutan) and *Lemuroidea* (lemur) (Craul et al. 2016, Eniang 2003, Rijksen et al. 1995) as well as other mammals, birds and fish (Lindenmayer and Fischer 2013, Perkin and Gido 2012). The leading cause of fragmentation is human interference through conversion of land use, urbanisation, deforestation and agriculture. Fragmentation is also caused by stochastic events and geological changes such as flooding, bushfires and erosion. Some theories speculate fragmentation is the cause of speciation from the restrictions of gene flow and lowering variability, however, full understanding of the implications that different levels of fragmentation hold is still lacking (Dias et al. 2012, Futuyma and Antonovics 1992). There is a wide variety of evidence which speculates that separation of populations leads to speciation (Rice and Hostert 1993, Fisher-Reed et al 2013), however, little is understood on the tipping points at which fragmentation becomes so great that speciation occurs. A species' biological traits will impact the tipping point, differing traits between species will cause fragmentation to have a varied level of impact and could mean there is no definable way to establish the tipping point (Hua and Wiens 2013). Although the physical effects of fragmentation have been demonstrated on the species that have been impacted, implications for the genetic dynamics of these species is not currently fully understood.

Genetic understanding has come a long way since Gregor Mendel first introduced the concept in 1865, from this stemmed the subfield of population genetics, which, with the help of modern technology, can be and now is widely studied. Genetic diversity among various taxa is becoming known as one of the most important factors contributing to the survival of species. Gene flow between populations is required to maintain variability, which is vital for species to adapt to changes within their environment (Slatkin 1987). The environment has a large influence on population genetics. Environmental changes restrict gene flow through preventing dispersal and lowering the variability between individuals and populations (Dubey and Shine 2010, Peacock and Smith 1997). Although this has been proven, there is still little information available of the environmental factors which contribute to changes in genetic variability. Smaller populations are known to suffer more from genetic diversity and variability loss due to limited genetic drift (i.e. when fragmentation or stochastic events occur) from larger populations (Frankham 1996). This can cause the disappearance of advantageous alleles over time, lowering the fitness of offspring and, in turn, lower the survival ability within the population (Whitley and Vose 2014). Limited genetic drift can also lead to speciation or, in extreme cases, extinction (Frankham 2005). Maintaining heterogeneity in populations is the goal of many geneticists. Lowering inbreeding and preventing homogeneity can only be done if the gene

pool is varied. As genes are lost, the chance of inbreeding increases, decreasing the survival and fitness of the species, therefore it is key to conserve as much of the gene pool as possible.

Primates are just one taxa that are highly impacted by fragmentation. They live in environments which are heavily threatened by deforestation and human encroachment which breaks the connectivity between habitats. Habitat connectivity is an issue conservationists try to maintain, it is understood that connectivity of all habitat varieties is necessary for species reproduction and survival (Ndimuligo 2007). Many primate species, both wild and captive are extensively studied; as many are keystone species (Mills et al 1993), the need to protect and conserve them is vital for maintaining the biodiversity in the regions they occupy. Although primates are extensively studied, genetic diversity and environmental effects on genetics is something that is often overlooked. It is crucial to recognise this as without it, the impact of conservation efforts cannot be fully understood and therefore might be seen as futile (Reed and Frankham 2003).

Life history strategies, home range size and dispersal distance play a key role in determining species survival and their adaptability to environmental changes (Agostini et al 2015, MacLarnon et al 2015). Reproduction, average age expectancy and inter-birth interval are required to understand the survival rate of a species (Dunbar 2013, Fleagle 2013). K-strategists; those which are long lived and have long inter-birth intervals, are likely to struggle with environmental and anthropogenic disturbances within their habitat (Caswell 1982). These species are adapted to living in a stable environment where raising offspring is expensive in terms of time and resources. Orangutans as K-strategists are known to suffer greatly with environmental changes due to mass reductions in the amount of suitable habitat they have available; many individuals are forced to survive in very fragmented and unstable environments (Nellerman 2007). With their inter-birth interval being the longest of all the apes (usually 7-9 years) (Galdikas and Wood 1990), the genus is left in a difficult situation when it comes to adaptability, especially during drastic environmental changes. From a genetic standpoint, adaptability is easily passed through generations when more offspring are produced annually/per birth. When selecting a mate, it is in most cases, the fittest individuals which are chosen first (i.e. those that are more adapted to their surroundings and are in better health). Therefore, in r-strategists, these characteristics and advantageous traits are selected sooner and further adaptations of these traits can continue to be altered through generations more rapidly than in those with long inter-birth intervals (Goddard 2008). The risks faced by r-strategists compared to those of a K-strategist which are situated in unstable environments are largely reduced. The majority

of primates are K-strategists which generates threat from environmental instability for most species, however, the few r-strategy primates such as *Microcebus* (Mouse Lemur) (Charles-Dominique 2012) may seem to be more adaptable to disturbance but they are still under threat from environmental changes making understanding adaptability crucial for conserving biodiversity. Comparing species with differing inter-birth intervals provides a wider knowledge on the adaptability of a species, discovering those which require conservation priority in relation to particular biological traits.

Home range size is another crucial factor governing the effects of fragmentation. Species with larger home ranges are likely to suffer heightened effects of fragmentation over those with shorter home ranges and dispersal distance, depending on the size of the fragments (Bunyan et al 2012). Fragment size has greater impacts on species with larger home ranges causing them to become isolated due to increasing rates of fragmentation (i.e. inability to overcome obstacles in their environment). Species with smaller home ranges may not have a vast enough home range for fragmentation to impact them directly, although if the rate of fragmentation is extreme it can effect both long and short ranged species equally (Marsh 2003). Dispersal and habitat restrictions negatively affect some genus' (e.g. *Pongo* and *Gorilla*), however, adaptability to extreme change in circumstance and environment is accounted for. With restrictions in habitat and dispersal distance, significant changes in behaviour, social structure and diet can be noted in species such as *Alouatta* and *Plecturocebus* (Chiarello and Galetti 1994, Chaves and Bicca-Marques 2016, Benchimol and Peres 2013). Although adaptations such as birthing more young more rapidly, having smaller and less specific home ranges and requirements and changes in behaviour and diet seem beneficial for survival in disturbed habitats, fragmentation and environmental changes can often cause implications to health and social living (Barelli et al 2015).

Social arrangement is a very important feature of survival. The benefits of social organisation includes protection, sharing of resources, access to mates and parental care. Species which are restricted in their home range may not have access to their required social arrangements, consequently lowering their chance of survival (Gould 1976). Understanding how home range size and dispersal distance is impacted for primates in fragmented environments is vital for understanding the scale of adaptability between species.

1.2 *Overview of Primates and Environmental Impacts*

Primates recover from disturbances at a very slow rate due to their long reproduction intermittence, late maturity and complex social arrangement. Fragmentation in populations of *Gorilla gorilla* and *Pan troglodytes* (chimpanzee) was explored in Cameroon. Construction of roads left *P. troglodytes* with only highland areas to survive in and no access to lowland portions of their environment. *P. troglodytes* were forced to retreat further into highland forest due to the continued construction of roads, however, these highland areas of forest contained vast signs of hunters which left *P. troglodytes* with little available suitable habitat. Over the three-year study, populations declined but remained stable in size and structure (Sunderland-Groves et al. 2003). A study by Chapman et al. (2006) found that small fragments cannot support *P. troglodytes* social groups, therefore the species would have to adapt to live in a similar social situation to that of *Pongo* in order to survive the current rates of deforestation. In a similar study, Silva and Ferrari (2009) discovered that *Chiropotes satanas* (bearded saki monkey) are able to survive in highly fragmented environments and often prefer disturbed habitats over primary habitat on some occasions. Although fragments were preferential, this change in environment came with consequences including; changes in behaviour, group size, home range and diet. Some of the main alterations seen between populations of *C. satanas* that were living in isolation include; increased time spent resting, less time spent travelling, less social interaction both intra-specific and inter-specific and a reduced group size of 7 members compared to the average of 30. It is thought these changes occurred due to the smaller home range, reduced group size and nutritional stress from diet changes (Silva and Ferrari 2009). This suggests that even species which are capable of surviving in highly disturbed and altered habitats still have to undergo drastic change to what would be deemed ‘normal’ in order to persevere and persist in the environment. As *C. satanas* is highly adaptable, other primates similar in size and life history traits may also be tolerant to changes, whereas, primates which are very different to *C. satanas* may have a diverse level of tolerance.

Gorilla gorilla are known to have recently undergone mass reductions in population size caused by hunting and the lack of suitable habitat, as a result, the species faced extinction (Tocheri et al 2016). Since then, maximum conservation efforts were enacted and abundance has increased (Stokes et al. 2010). With this major decline comes a genetic bottleneck, these bottlenecks can cause species to be deficient in the genes they require in order to survive which can cause negative mutations, sometimes leading to speciation (Nei et al. 1975). In *G. gorilla*, the effects of this bottleneck are not yet understood and how it may affect the future survival of the species is unknown. Other primate species are

currently under serious threat and could soon face the same future as many *G. gorilla* populations, therefore a need to understand environmental pressures and how they play a role in the genetics and survival of the species comes into action.

Many primates are impacted by fragmentation, some of which (*Pongo, Gorilla*) are endangered and at risk of furthering habitat loss and destruction. However, genetic variability in remaining populations and changes to gene distribution due to heavy environmental pressures is still yet to be understood. As some species (*C. satanas, Aloutta palliate* (howler monkey)) are known to be more adaptive in pressured environments, it could suggest that some primates opt to change their natural desired mating partners in order to select traits which are more suitable for survival in the current rates of environmental change. Selecting partners to optimise survival will have serious impacts on the already established gene distributions throughout populations which could lead to isolation of genotypes, this has already happened for metapopulations of *G. gorilla* where inbreeding and homozygosity are increased due to long-term population decline (Xue et al 2015). This could also mean that previously 'unfit' individuals (e.g. those which are not healthy or not suited to their environment) are chosen over mating partners which have a more varied gene pool and will generate healthier offspring. A study by Mbora and Mcpeek (2014) investigated genetic diversity among *Procolobus rufomitratus* (colobus monkey) and *Cercocebus galeritus* (mangabey) through analysing allelic richness and heterozygosity. *C. galeritus* had the highest allelic richness and heterozygosity although both species had approximately equal overall genetic diversity. In both species, heterozygosity was high but allelic richness was low. This is indicative of very little inbreeding but small-scale gene flow meaning only a minor selection of genes are entering each metapopulation. *C. galeritus* was also the only species that persisted in isolation by distance, suggesting that this species is much more adapted to its environment than *P. rufomitratus* even though genetic diversity is similar (Mbora and Mcpeek 2014). Primates are already seen to be suffering from genetic diversity and variation loss without the additional pressures caused by environmental factors. Therefore, understanding these impacts comes into major importance in discovering how the taxa may survive in the future.

1.3 *Modelling*

Collecting genetic data from wild populations is difficult, time consuming and costly, it is much easier to replicate the situation in question in the form of a model. Even if not completely accurate, it forms a basis for further study by giving a proposed scenario and

hypothesis for the results that would be expected from undertaking the study in-field. Models are commonly used for a wide range of scientific studies, especially when determining population ecology and dynamics. As well as producing testable predictions, extreme and risky circumstances (and those which might not or cannot be implemented in-field) can be modelled to offer future projections for worst case scenarios (Evans et al 2013). Many models are often used as a broad framework for expressing realistic and unrealistic circumstances. The model used for this study creates realistically simulated individuals that behave in a certain way to mimic general behaviours of a wide range of species. In this case, primate is the taxa of choice, therefore, individuals within the model behave approximately like primates. This offers a realistic approach to aid the understanding of environmental impacts on the genetic diversity of primates without causing unnecessary harm to the taxa and their habitats. As many primates are already facing threats, it is much more effective and efficient to use models to gather genetic data than increase anthropogenic pressures for the taxa. Using models also lowers disturbance in previously undisturbed or relatively intact habitats which again, increases the quality of the habitat for the taxa whilst still providing valid and valuable results.

1.4 *Aims, Objectives and Hypothesis*

The aim of this study is to explore environmental effects and the impacts they hold on the genetic variability of primates with a 2 or 5 year inter-birth interval to discover which environmental factor has the greatest impact. This was undertaken through the creation of an individual-based model. A scenario similar to those for wild primates was created and the genetic information was provided in the output of the model. The model uses; 1) fragmentation; and 2) habitat cover as environmental factors; 3) life history traits (e.g. 2 or 5 year inter-birth interval); 4) number of individuals; and 5) dispersal distance, as biological factors. It is hypothesised that all of these factors will lead to changes in genetic variability. Each environmental factor is analysed individually to determine direct impacts and again with 2 or more variables to determine indirect and dependant impacts. Allelic richness and heterozygosity are used to determine overall diversity between populations at various levels of effect. The results will be applied to primates which match the model criteria (e.g. similar in birth, death, inter-birth interval rate and habitat) using available literature to discuss impacts differing species might face. By comparing the genetic output of species with different reproduction rates, environmental impacts can be further understood providing information on how species may need to adapt to survive. Many primates require urgent conservation attention, those which may be impacted but can

maintain a healthy gene pool do not need to be prioritised whilst others which face current and often extreme rates of environmental and biodiversity loss need prioritising.

2.0 Methods

2.1 *The Model*

The model used was adapted from the AlleleScape model by Jackson and Fahrig (2014); a spatially explicit individual-based model created using Netlogo 4.1.3. It was adapted to make the hypothesised situations which are entered into the model more suited to the study question and to create a more realistic situation for primates. The updates to the model include: 1) Maximum age of individuals; 2) Number of offspring produced by each individual; 3) Birthing interval; 4) Movement of males; 5) Sexual maturity age; 6) Random ages upon start; and 7) Updated to perform in the newest version of Netlogo 5.3.1. The model simulates birth, dispersal, mating, reproduction, and death of individuals in stochastically generated heterogeneous landscapes. The model was used to simulate situations for 10 different species of primates that each varied in dispersal distance (*Dav*) and reproductive interval (2 or 5 years), each scenario interacted with 25 types of landscape that differed in habitat fragmentation (*H*) and habitat coverage (*P*). The impact of each landscape characteristic on genetic diversity was investigated.

Landscape simulations were generated randomly with habitat coverage and fragmentation determined by sliders at the setup of each simulation. The proportion of habitat fragmentation varied between 0.1, 0.3, 0.5, 0.7 and 0.9. High values of fragmentation (e.g. closer to 1) indicate a less fragmented environment and low values (e.g. closer to 0) indicate more fragmentation, the inverse was used as the model determines 'clumpiness' rather than level of fragmentation and therefore at higher values the landscape was more clumped together than fragmented. The values for *P* in the model were the same as those for *H*, however these values were not inversed and 0.1 indicated 10% habitat coverage within the landscape, values of 10%, 30%, 50%, 70% and 90% were used. For example the setup *P*=0.1 and *H*=0.1, would simulate 10% of suitable habitat with a high rate of fragmentation. Each landscape was composed of a 101x101 cell grid and a random landscape shape was simulated within this grid according to the specified *H* and *P*. Each simulation used a different randomly selected landscape from a group of pre-determined settings.

2.2 *Model setup*

Each simulation is initially populated with 100 individuals. At the start, individuals are randomly assigned throughout the landscape without accounting for habitat structure, this is in order for populations to gather in suitable habitat after initial dispersal. Each

individual is assigned with five diploid loci and a random gene copy out of the possible 20 alleles available for each locus. Replication of 20 allele types at 5 loci is a representative proportion of the gene pool found in non-simulated situations. Individual sex is assigned randomly with a 1:1 ratio to provide equal opportunities upon starting the model and avoid skew in the data. Each individual is assigned a random age between 0-35 years at the start of the model to simulate a more realistic population dynamic.

To simulate movement, each individual moves one step (one cell) in a random direction every turn (tick) across a continuous habitable surface. Although female influenced dispersal is common in various taxa (e.g. birds and insects) (Strokes et al 2003), random dispersal of both males and females was used in order to maximize the effects seen by *Dav*, *P* and *H*. This also reduces the potential for small groups to gather in unsuitable habitat at the start of the model, prevent isolation and future dispersal into unsuitable habitat. Dispersal distance was calculated from a negative exponential distribution which provides the mean equal to the specified *Dav* given at the start of the model. *Dav* was varied between 2, 4, 6, 8, or 10 cells per simulation, this was to account for an individuals dispersal potential and their relationship with landscape structure.

After initial dispersal has taken place, each female over the age of 10 is given the opportunity to reproduce with either the closest male within radius of *Dav* or a random male in the radius. In these simulations each female reproduced with the closest male in order to maintain continuity and further ensure mating opportunity. During the experimental runs, having females mate with a random male had no effect on results, although this may not always be the case as this factor is dependent on the situation being simulated. If no male is available in the radius of *Dav* or the female is located within the focal site, she does not mate on this turn. By formulating this setup, it simulated a polygynous mating system; more than one female can mate with the same male in a single turn and only have one reproductive partner whereas males have the opportunity to mate multiple times if possible. This simulated a more realistic mating strategy as the majority or primates are polygynous which makes the model more suitable. The number of offspring a female produced per parturition was calculated using a Poisson distribution, a rate of 0.18 was used as most primates birth between 1-2 offspring each parturition (Charnov and Berrigan 2005), this gives a 0.18% chance of a female producing more than 1 offspring at a single time. The following logistic growth equation (Law et al 2003) was also used to calculate the mean growth rate; where population growth (λ) and carrying

capacity of a cell (K) were both set at 1 for all simulations. $^{N}_{F}$ is the number of females occupying a cell at any given time.

This attained a steady population during the use of landscapes with low habitat and high fragmentation and a manageable growth rate in high habitat and low fragmentation landscapes. Once females are fertilised, they give birth on the next turn but cannot reproduce again for another 2 or 5 years (ticks) to simulate the inter-birth interval. Offspring occupy the same cell as their mother until they reach the age of 5, at this age they randomly disperse using the same movement strategy as the adults. Each offspring is randomly assigned a sex at the beginning of the turn it was birthed. Upon birth, the offspring inherit one allele from each parent for each five loci. A K-allele mutation model was undertaken to determine the rate of mutation, this gives each allele an equal probability of mutating. Mutation rate was set at 0.0001 which is common for multiple species (Bhargava and Fuentes 2009).

$$F = 2\left[\frac{\lambda}{1 + \left(\frac{\lambda - 1}{K}\right)N_F}\right].$$

After reproduction, adults have the opportunity to reproduce again after waiting their specified inter-birth interval where as juveniles disperse and have the opportunity to mate when they reach maturity at age 10. All individuals die at the age of 35, however, males can continue to reproduce until they reach the age of 35, whereas, females can only reproduce up until the age of 31 as offspring will not disperse until the age of 5 and will not survive without their mother present under the age of 5.

2.3 *Simulation experiments*

Two main experiments were carried out to test the full spectrum of impacts that *P*, *H* and *Dav* have on different landscapes and population dynamics. In both experiments habitat amount, fragmentation and average dispersal distance were individually set at 5 different levels each, giving 125 factor based combinations for each experiment (totalling 250). Each combination was repeated 5 times using a different random landscape, the average per 5 runs provided the overall total allelic variation for each individual simulation. The model was run for 100 generations to provide enough time for populations to grow and stabilise for validation of the genetic equilibrium. If populations went extinct the data was discarded and the model was either ran again (depending on extinction time) or less runs were used to calculate the average. If the population went extinct before 50 generations, the data was not used, after 50 generation the model was ran again. A ‘stopearly’ timer was used within the model; if the landscape did not contain a viable or breeding population for 30 turns, the run was terminated and a new landscape was assigned before re-trying the

model with the same factor settings. In preliminary simulations, when the landscape contained too few individuals, populations would not recolonise and therefore, to save run time, the 'stopearly' was added. To get a full scale of environmental effects each 125 factor combination set was used where females have a 2 year inter-birth interval and again for a 5 year inter-birth interval. Results were collected from genetic variation expressed throughout the entire landscape.

2.4 *Model output*

Allelic richness for the entire landscape is collected and used to determine genetic diversity of the remaining individuals after 100 turns. Genetic diversity is given with 2 outputs; allelic richness (*A*) and expected heterozygosity (*He*). Population size is recorded throughout the model to define alterations of genetic variation through fluctuations in abundance (*N*). The inbreeding coefficient is also provided in the output of the model (*FIS*) to track deviations from observed heterozygosity due to random mating *(FIS = He [He/Ho]*). Populations are recorded every 5 or 2 turns for 100 turns amounting to 100 generations. Data is recorded from the start of the model and is collected from every juvenile (e.g. those which are under 10 years of age) to be able to appropriately analyse difference in genetic diversity from the starting population. The final recording is taken at 100 turns giving the ending genetic diversity, this is used to determine genetic deviations from the source population. The final output is calculated from the averages of *A*, *He* and *N* during each run of the model at the 125 adjustable variable combinations for both 2 and 5 year inter-birth interval.

2.5 *Statistical analysis*

Relationships between *P*, *H* and *Dav* with the three outputs *N*, *A* and *He* were analysed in SPSS 23 using two-way ANOVA interactions. Logistic regression was also used to determine relationships between each of the variables and model outputs. Various Q-Q plots to test for normality were created and multiple scatter plots were made to visually represent the results, as well as easily showing any linear trends. Akaike information criterion (AIC) was used with *P*, *H* and *Dav*, and again testing just the 2 main variables *P* and *H*. As repeated results can lead to false or increased significance even if the results are not, when using logistic regression the sum of squares (%SS) was used rather than significance level to avoid false significance.

3.0 Data Results and Analysis

3.1 *Results*

Scatterplots including all environmental variables to look for relationships in each variable when tested together were created as the AIC score was lowest (518.179) when the three experimental variables were included. All environmental factors combined were first tested against each model output to measure diversity and discover if these variables influence each other as a first step towards testing all hypotheses. After creating Q-Q plots (appendix III) to determine normality of data it was discovered that all data was non-normally distributed and did not match the expected values, therefore non-parametric tests were undertaken to analyse data. *H* was not inverted in figures 1 to 6 to make data representation easier to interpret, but is inverted in the remaining results.

Where *H* is lower, *A* is higher (figure 1 and 2) where *H*=0.1 and *H*=0.9, *A* is higher. Comparing the 2 year to 5 year inter-birth interval, *A* is much higher with a lower inter-birth interval, allelic richness at *Dav*=2 is lower but increases by *Dav*=4, whereas with a longer inter-birth interval (5 year) (figure 2) allelic richness deviates a little peaking at *Dav*=6. With a 2 year inter-birth interval (figure 1) allelic richness increases much more linear with increasing habitat amount and dispersal distance than a 5 year interval.

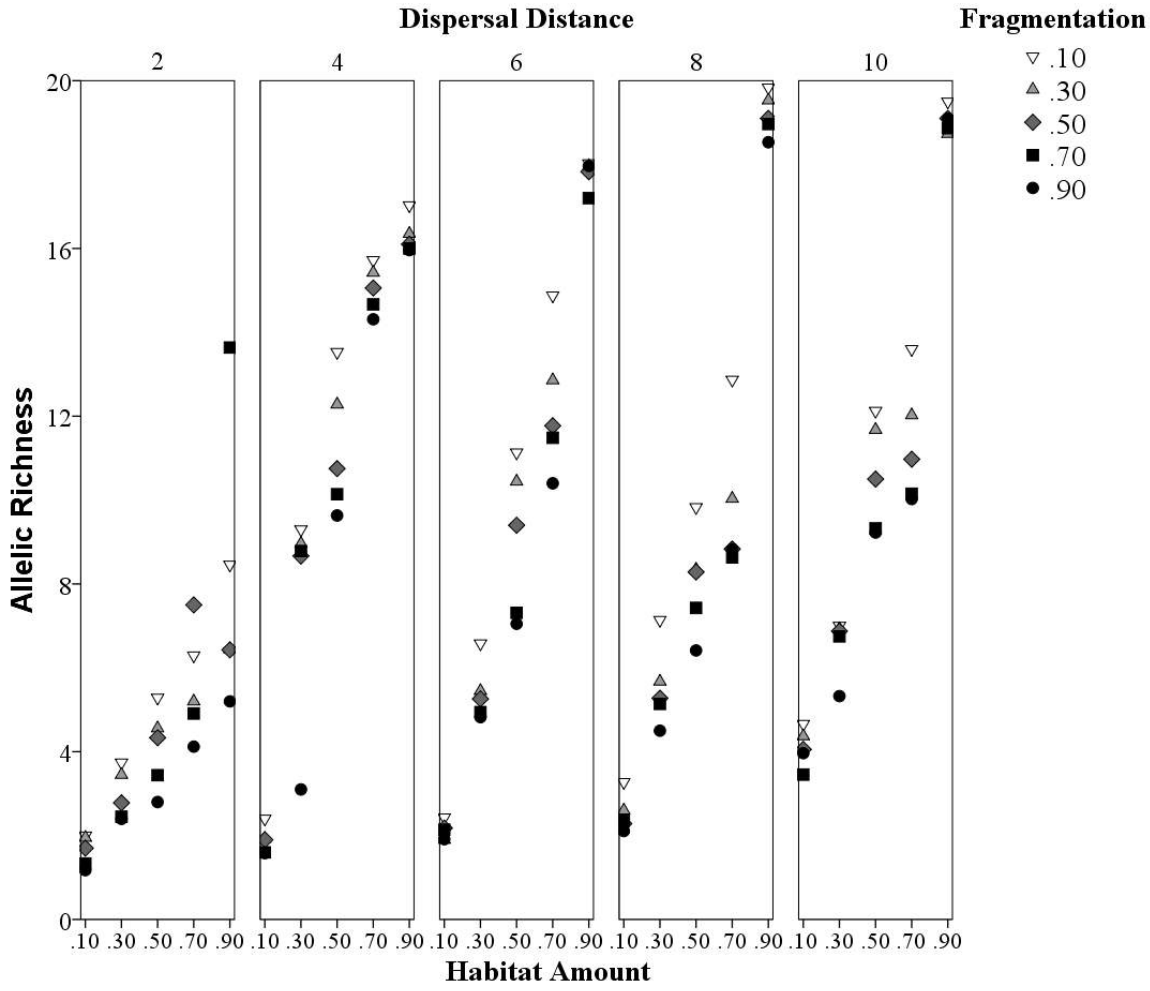

Figure 1 – Average genetic variation expressed by allelic richness (A) plotted against habitat coverage/amount (P), average dispersal distance (Dav) and different levels of habitat fragmentation (H) for 2 year inter-birth interval.

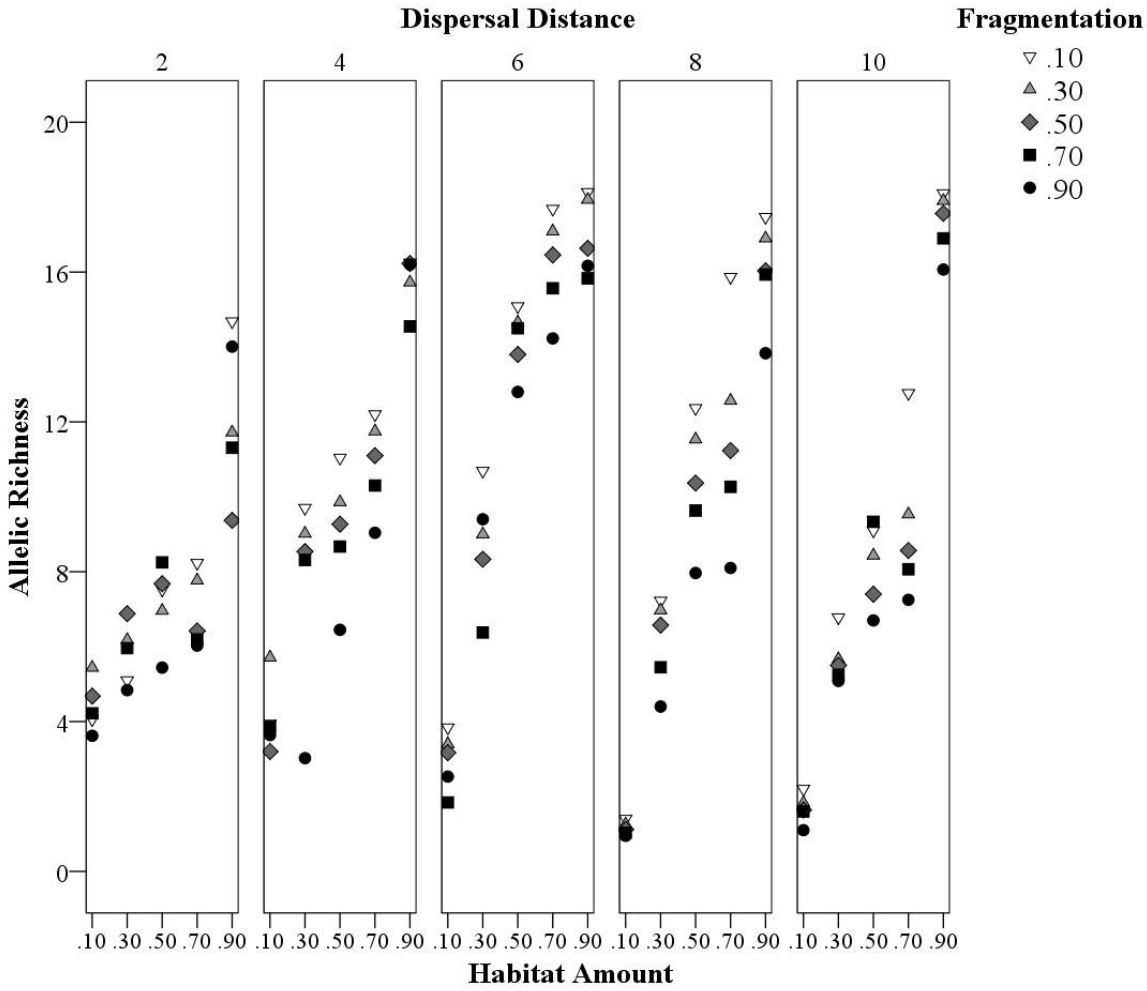

Figure 2 – Average genetic variation expressed by allelic richness (A) plotted against habitat coverage/amount (P), average dispersal distance (Dav) and different levels of habitat fragmentation (H) for 5 year inter-birth interval.

The effects of each environmental variable were also tested against population size (figure 3 and 4) and heterozygosity (figure 5 and 6) to investigate if these factors hold indirect effects on genetic diversity by altering *N* and *He* independently. With a 2 year inter-birth interval, habitat amount highly impacted population size (figure 3), *N* was much more varied with increased *H* and *Dav* but a positive linear relationship was seen at each dispersal distance. Population size increased with a higher dispersal distance, but became much more varied with increasing environmental factors. The opposite effect was seen with a 5 year inter-birth interval (figure 4), *N* started off much more varied with lower environmental variables and as *P*, *H* and *Dav* increased, *N* became condensed and linear.

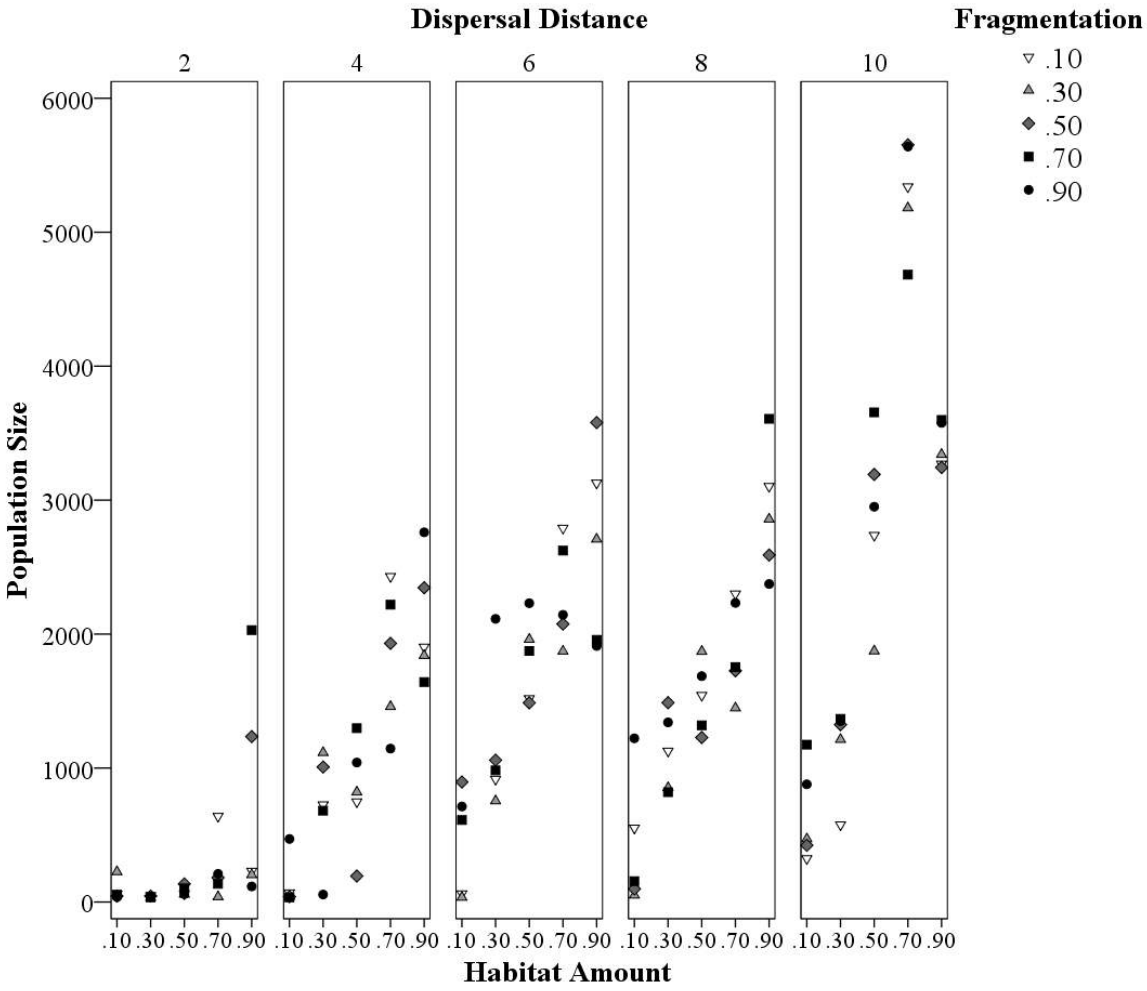

Figure 3 – Average population size expressed by allelic richness (N) plotted against habitat coverage/amount (P), average dispersal distance (Dav) and different levels of habitat fragmentation (H) for 2 year inter-birth interval.

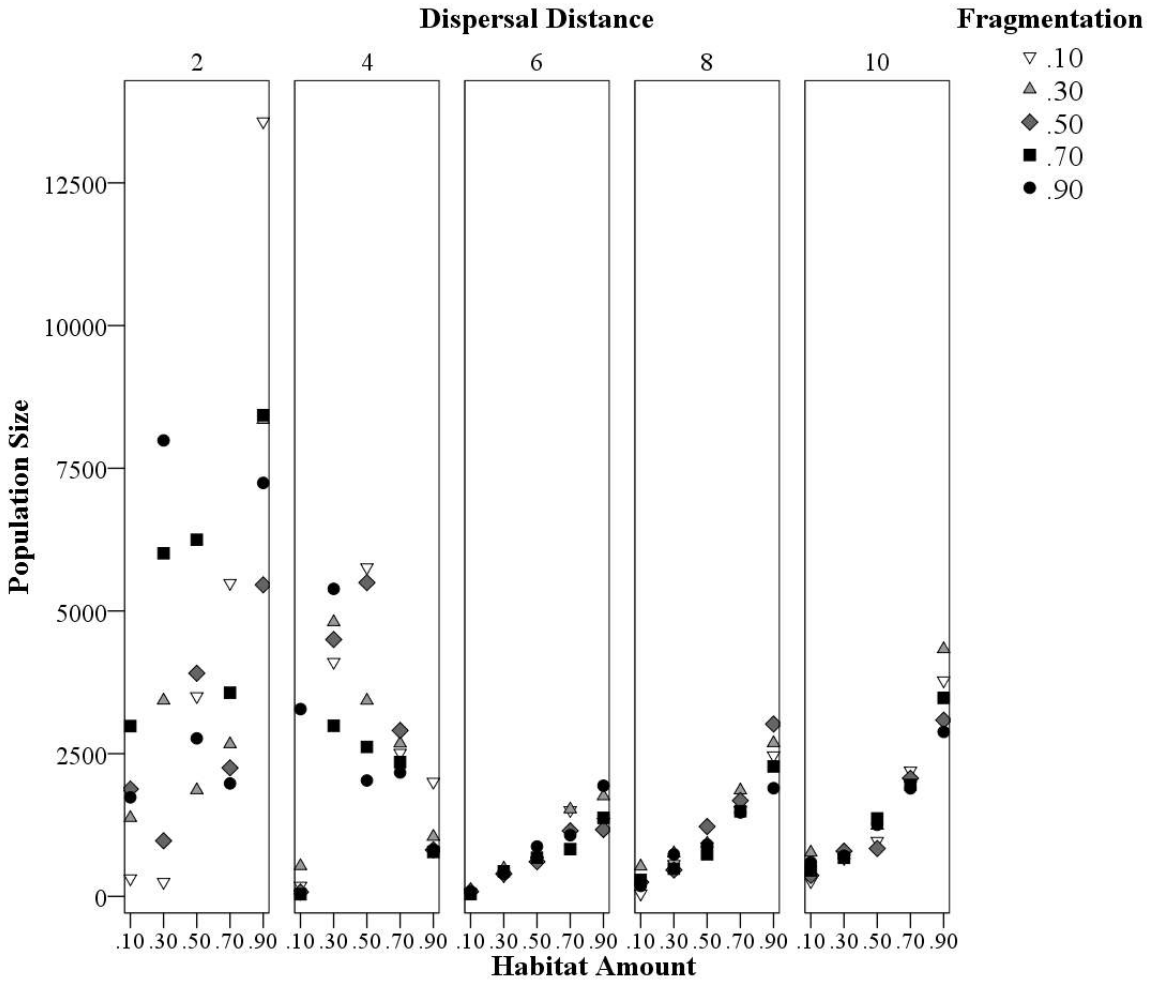

Figure 4 – Average population size expressed by allelic richness (N) plotted against habitat coverage/amount (P), average dispersal distance (Dav) and different levels of habitat fragmentation (H) for 5 year inter-birth interval.

Heterozygosity for both a 2 and 5 year inter-birth interval was very varied with *Dav*=2 and 4, however it was much more linear after these dispersal distances and both 2 and 5 year inter-birth interval results did not differ too much. Allelic richness *(He)* increased with habitat amount but dispersal distance and fragmentation held very little effect (figure 5 and 6).

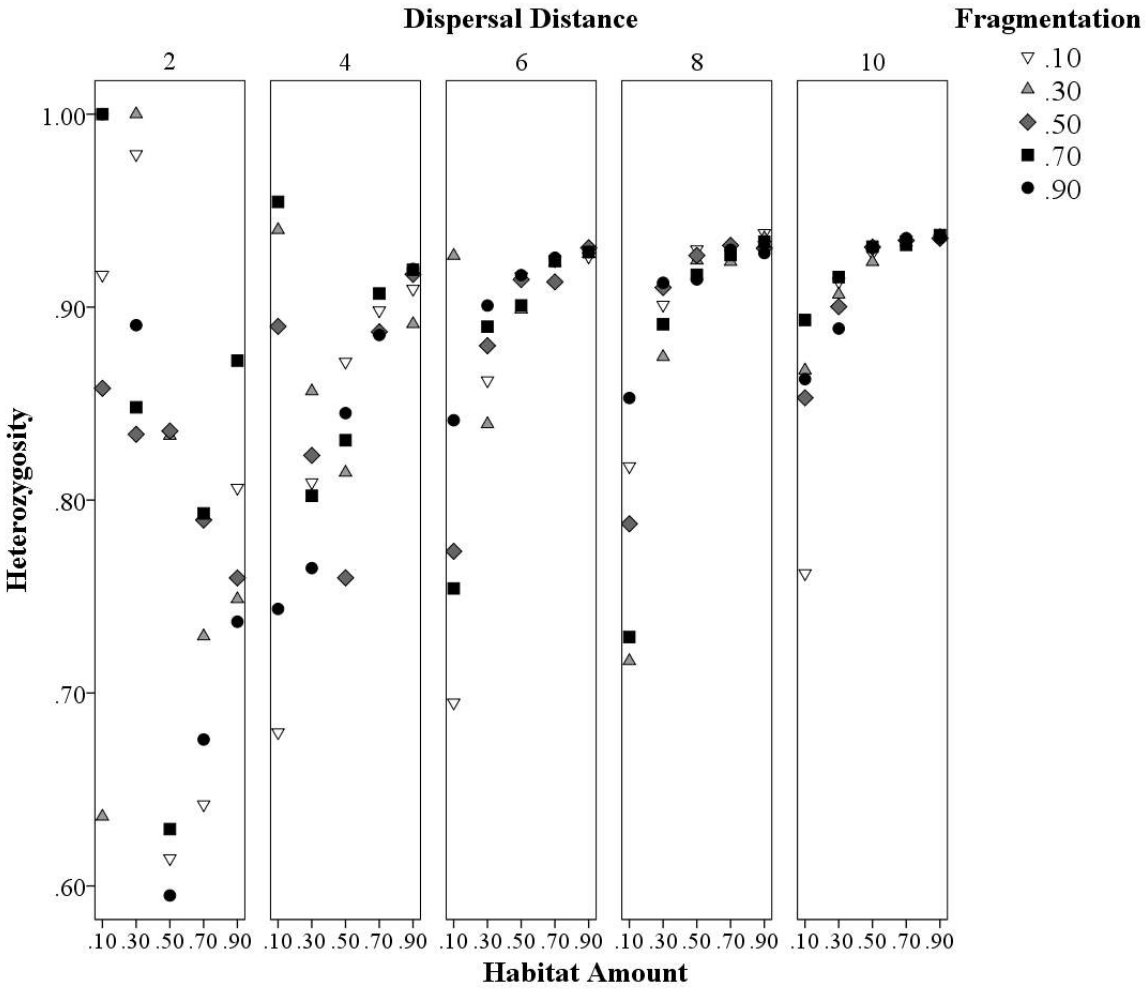

Figure 5 – Average heterozygosity expressed by allelic richness (He) plotted against habitat coverage/amount (P), average dispersal distance (Dav) and different levels of habitat fragmentation (H) for 2 year inter-birth interval.

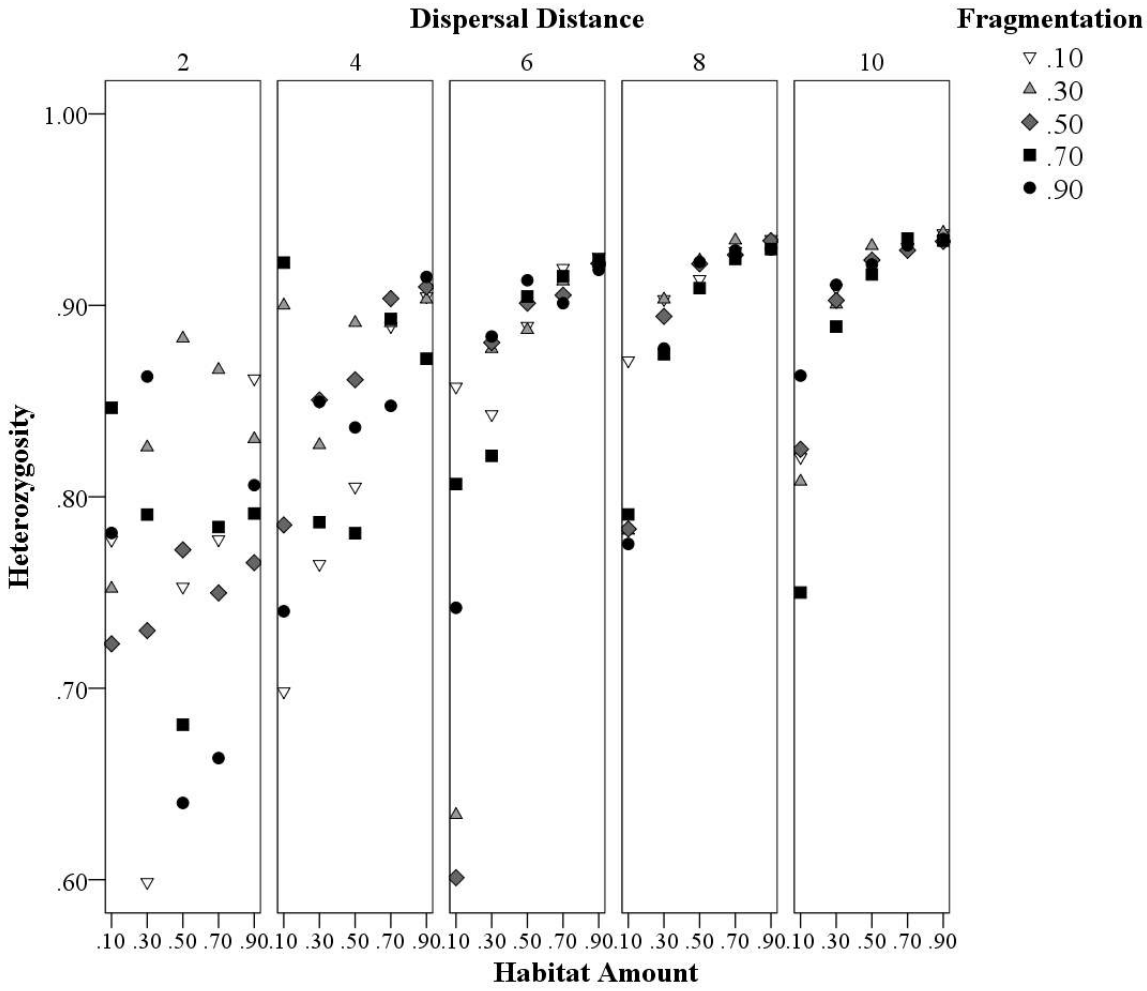

Figure 6 – Average heterozygosity expressed by allelic richness (He) plotted against habitat coverage/amount (P), average dispersal distance (Dav) and different levels of habitat fragmentation (H) for 5 year inter-birth interval.

Logistic regressions were used to analyse the effects of each environmental variable combination with all dependant variables. To avoid false significance, the percent sum of squares (%SS) was calculated and significance values were taken from this.

P held the highest influence on *A* (table 1) with a 2 year inter-birth interval with *P:Dav* having the second biggest impact and *Dav* having the third most significant impact (25%). Another significant result in the data is the negative impact that *H:Dav* had on allelic richness (-11%).

P:Dav had the greatest influence on population size, however, *H* has a strong negative impact on *N*.

All variables generated very similar (16-18%) results when tested for effects against heterozygosity but *H* had the greatest impact, variables all held an equal impact. Although some of these results contradict previous bi-variate analyses, they follow the expected and predicted R-squared results.

Similar results were found with a 5 year inter-birth interval with *P, Dav* and *P:Dav* again holding the highest impact on *A*, however, these three variables have a similar level of impact as difference between the results is small (6% difference compared to a 19% difference with a 2 year inter-birth interval). *H:Dav* did not have a negative impact on *A* here and results were not significant.

Dav and *H:Dav* both had the same level of impact on *N* and no variable had any negative results suggesting that all variables here positively impact population size. Habitat amount had the least impact on population size.

Much like the 2 year results, all variables held an equal impact on heterozygosity with a 5 year inter-birth interval, with *H* again holding the largest impact, however, *P:Dav* had a slightly lower result.

Table.1 – Logistic regression of A, N and He when tested against all possible environmental variable combinations with (%SS) for both 2 year (left) and 5 year (right) inter-birth interval.

	A (%SS)	*N* (%SS)	*He* (%SS)
P	44%	-18%	17%
H	3%	-285%	18%
Dav	25%	29%	16%
P:H	8%	4%	17%
P:Dav	31%	318%	16%
H:Dav	-11%	51%	16%

	A (%SS)	*N* (%SS)	*He* (%SS)
P	30%	4%	17%
H	5%	15%	18%
Dav	24%	29%	16%
P:H	9%	5%	17%
P:Dav	28%	18%	15%
H:Dav	3%	29%	16%

Two way ANOVA results indicate that *H* had a highly significant impact (P = 0.000) on allelic richness but no impact on any other variable for a 2 year inter-birth interval (table 2). *P* did not directly impact *A* but a highly significant impact was seen with *N* and *He* (P = 0.000). Heterozygosity and population size significantly impacted each other (P = 0.000) on the same level demonstrating that these have a direct two way relationship, with *P* being the only single highly influential variable of *He* that wasn't dependant on any other factor. *Dav* had a very significant influence on all dependant variables (P = 0.003 and 0.000). No other significant results were seen, however, as *P*, *Dav* and *N* all impact *N* and *He*, an indirect effect on genetic diversity may be possible.

The 5 year inter-birth interval ANOVAs expressed that *H* (P = 0.000) and *N* (P = 0.026) both have a significant effect on allelic richness, *P* is not significant (P = 0.053), however, the figure is close to 0.05 so will have some impact on *A*. *P* and *Dav* are significant indicators of *N* (P= 0.000), *A* also had a slight impact but *A* and *N* depend on each other for the effect to take place. *P* and *Dav* are the only factors influencing *He.* Since no other

significant results were found, this does not exclude the possibility that factors may still effect genetic diversity indirectly through having a significant impact on any of the dependant variables.

Table.2 – Two way ANOVA P-value results of each possible environmental factor including population size of allelic richness for both 2 year (left) and 5 year (right) inter-birth interval.

	A (% SS)	*N* (% SS)	*He* (% SS)
P	0.148	0.000	0.009
H	0.000	0.622	0.653
Dav	0.003	0.000	0.000
N	0.102	-	0.000
A	-	0.102	0.114
He	0.114	0.000	-

	A (% SS)	*N* (% SS)	*He* (% SS)
P	0.053	0.000	0.000
H	0.000	0.920	0.695
Dav	0.571	0.000	0.000
N	0.026	-	0.302
A	-	0.026	0.604
He	0.604	0.302	-

3.2 *Hypothesis 1 – Population Size*

To understand any effects that each variable had on genetic diversity and to see which one may have the highest effect, each environmental variable was tested against allelic richness individually including dispersal distance. Although dispersal distance is not hypothesised to impact genetic diversity, it was tested to discover if the other experimental factors (*P*, *H* and *N*) were individually effecting genetic diversity or if each variable relied on each other. The first hypothesis predicts that population size will lower genetic diversity. A relationship between population size and allelic richness (figure 7 and 8) was not found with a 2 or 5 year inter-birth interval. Although the R-squared values (Spearman's Rho=0.022 and 0.040) are indicative that *N* is not a significant indicator of allelic richness, a positive relationship with a 2 year inter-birth interval was predicted and a negative relationship with a 5 year interval. This important difference between the inter-birth intervals indicates that *N* may have an indirect impact on allelic richness when other variables are present.

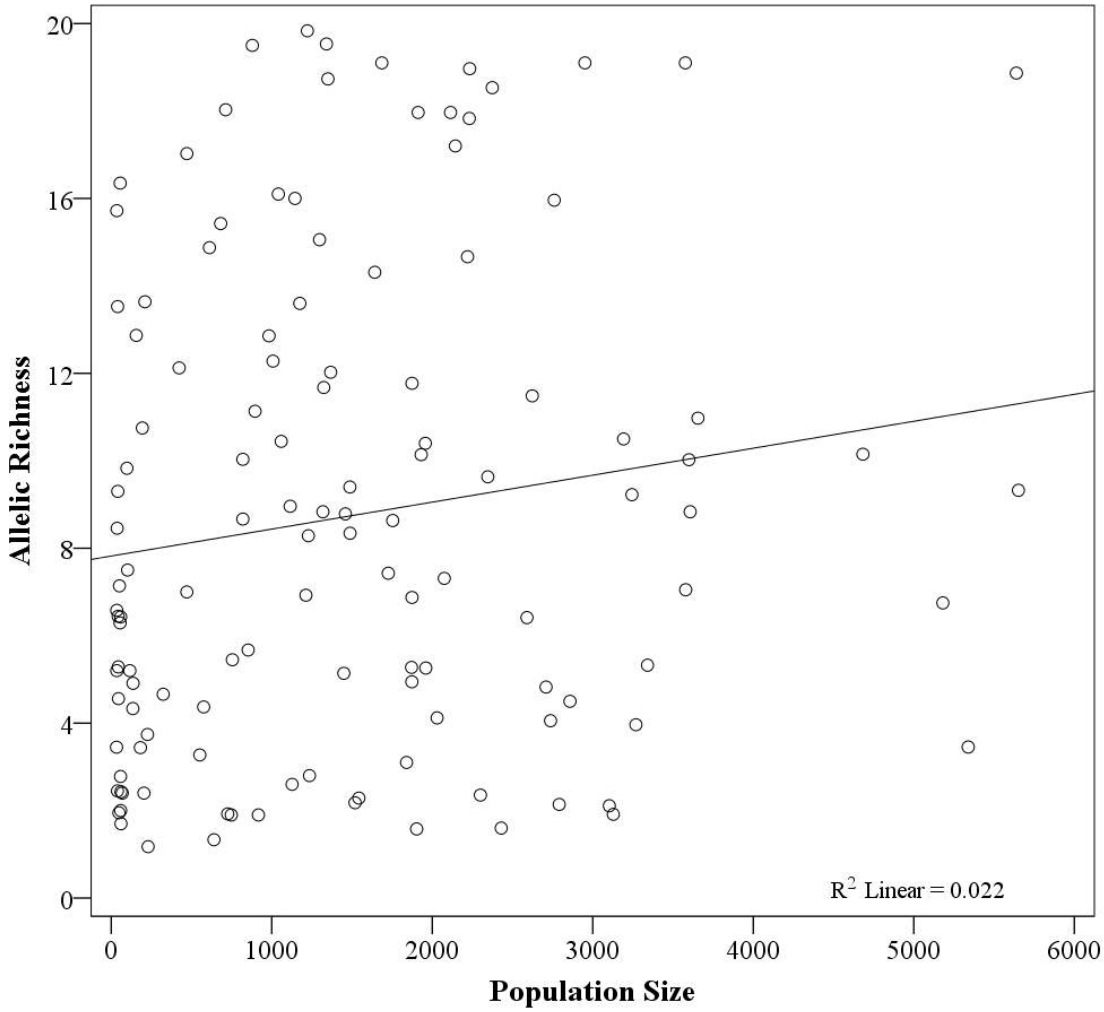

Figure 7 – Allelic Richness (A) plotted against population size (N) for 2 inter-birth interval. R-squared value = 0.022.

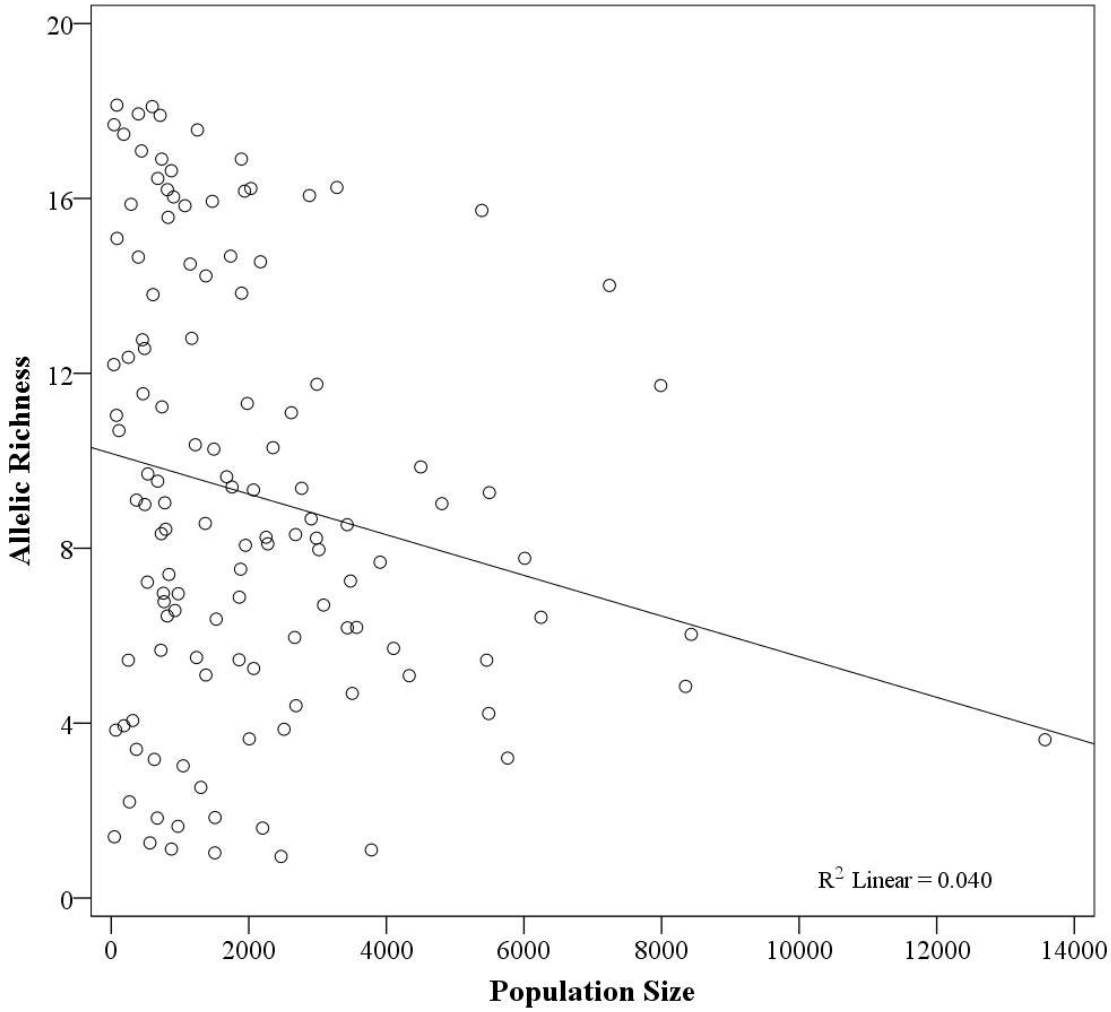

Figure 8 – Allelic Richness (A) plotted against population size (N) for 5 inter-birth interval. R-squared value for 5 year = 0.040.

3.3 *Hypothesis 2 – Fragmentation*

The second hypothesis predicts a more fragmented environment will lead to lowered genetic diversity. A strong positive linear relationship was found between *A* and *H* for both 2 and 5 year inter-birth interval (figure 9 and 10). This variable has a very significant (R^2 = 0.698) impact and is the biggest predictor of genetic diversity. Fragmentation had a higher impact with a 2 year inter-birth interval with low results when *H*=0.1 and sufficiently rises with each level of *H* (figure 9). This effect is seen again with a 5 year inter-birth interval (figure 10), however, difference in increase is not as high with each level of *H* as it is for 2 year.

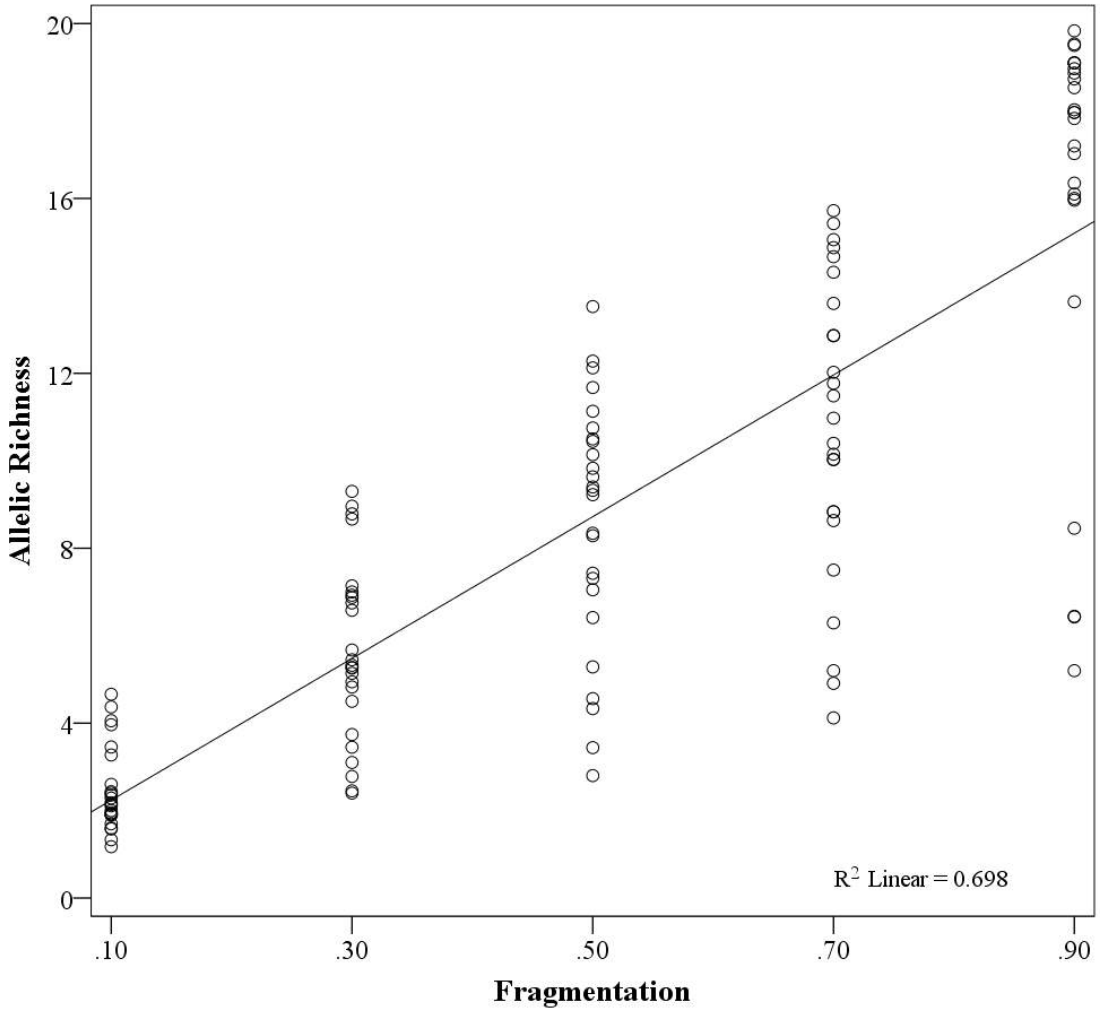

Figure 9 – Allelic richness (A) plotted against habitat fragmentation (H) for 2 year inter-birth interval. H is inverted (1-H). R-squared value = 0.698.

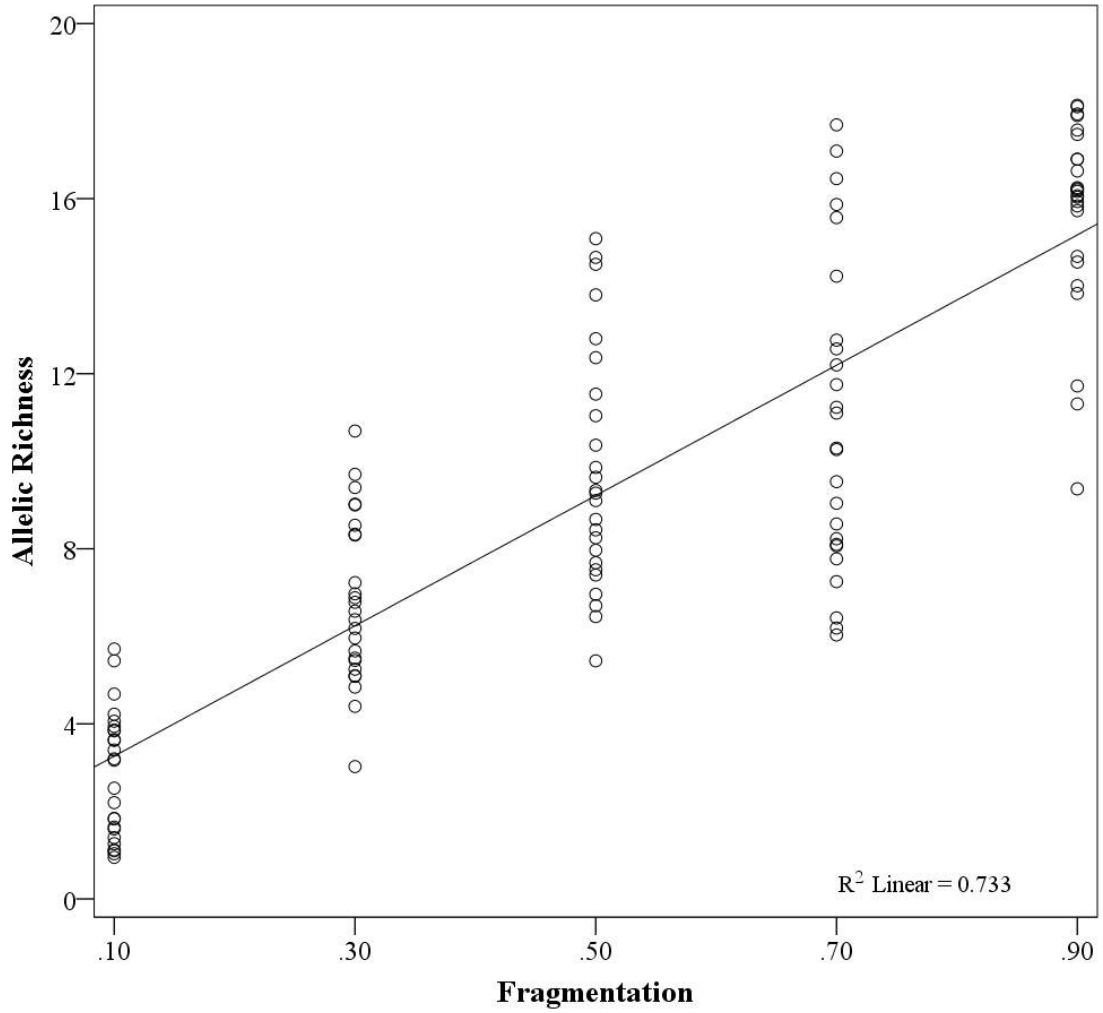

Figure 10 – Allelic richness (A) plotted against habitat fragmentation (H) for 5 year inter-birth interval. H is inverted (1-H). R-squared value =0.733.

3.4 *Hypothesis 3 – Habitat Amount*

The third hypothesis predicts that habitat amount will impact genetic diversity, more habitat coverage will increase diversity (figure 11 and 12). Similar to the *N* results, habitat amount was very varied and there was no clear trend, however, the R-squared values (Spearman's Rho=0.017 and 0.030) predict a weak negative relationship with the data, again this could indicate that *P* has a significant effect when used alongside other variables but is not significant individually. The linear regression lines suggest that habitat amount has a greater effect on species with a 5 year inter-birth interval with the data having a better fit to the line (figure 12). In both 2 and 5 year inter-birth interval species, the data is highly variable, in the 5 year results the data are slightly more condensed around centre value of *A* (8-10).

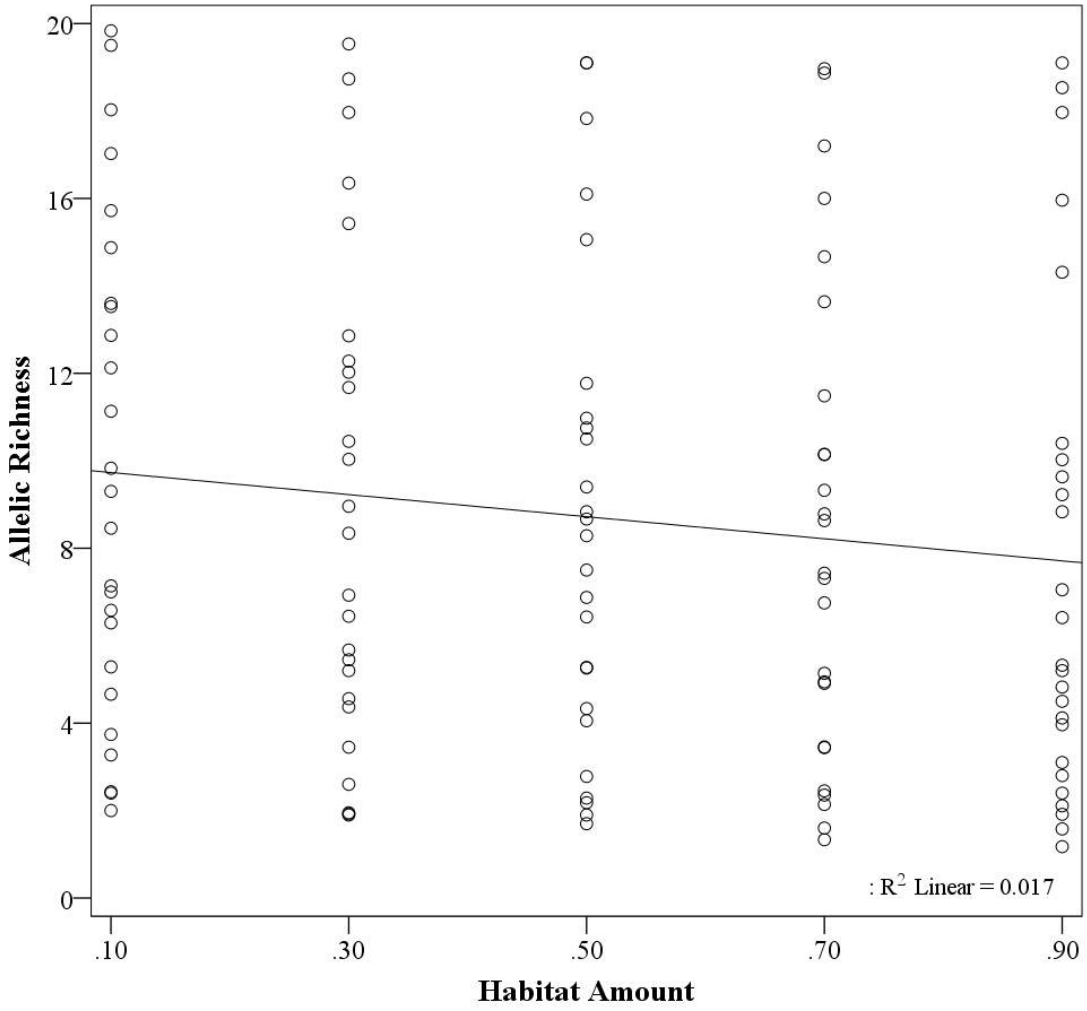

Figure 11 – Allelic richness (A) plotted against habitat amount (P) for 2 year inter-birth interval. R-squared value for 2 year = 0.017.

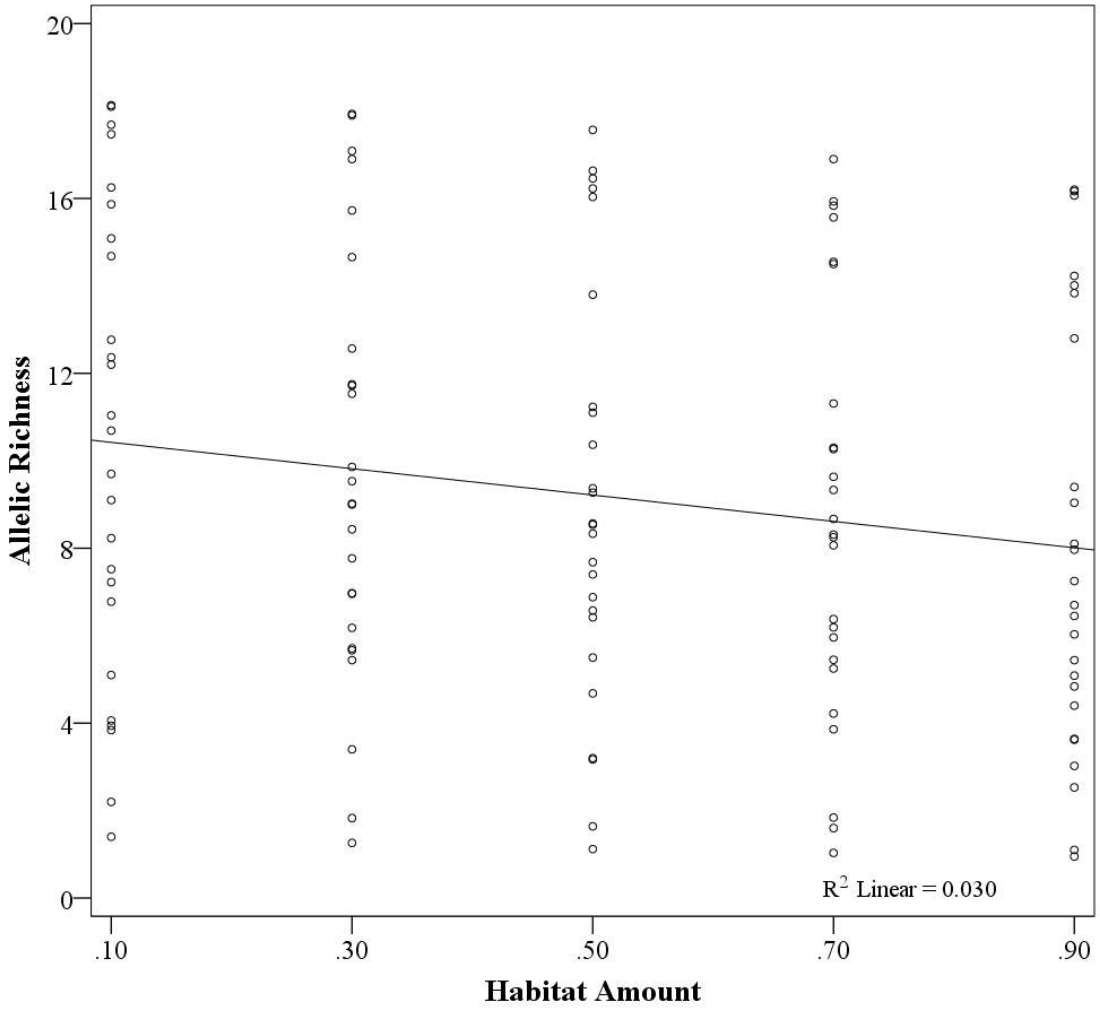

Figure 12 – Allelic richness (A) plotted against habitat amount (P) for 5 year inter-birth interval. R-squared values for 5 year = 0.030.

3.5 *Additional data*

Additionally, dispersal distance was tested against allelic richness. Similarly to previous results, there were no clear relationships between these two variables (figure 13 and 14) but the R-squared values (Spearman correlation: Rho=0.071 and 0.003) indicate there was a slight positive relationship. For a 2 year inter-birth interval, dispersal distance had a slightly more positive trend suggesting again that this may have an effect when tested with other variables. The 5 year inter-birth interval linear regression line predicts virtually no trend between allelic richness and dispersal distance (figure 14).

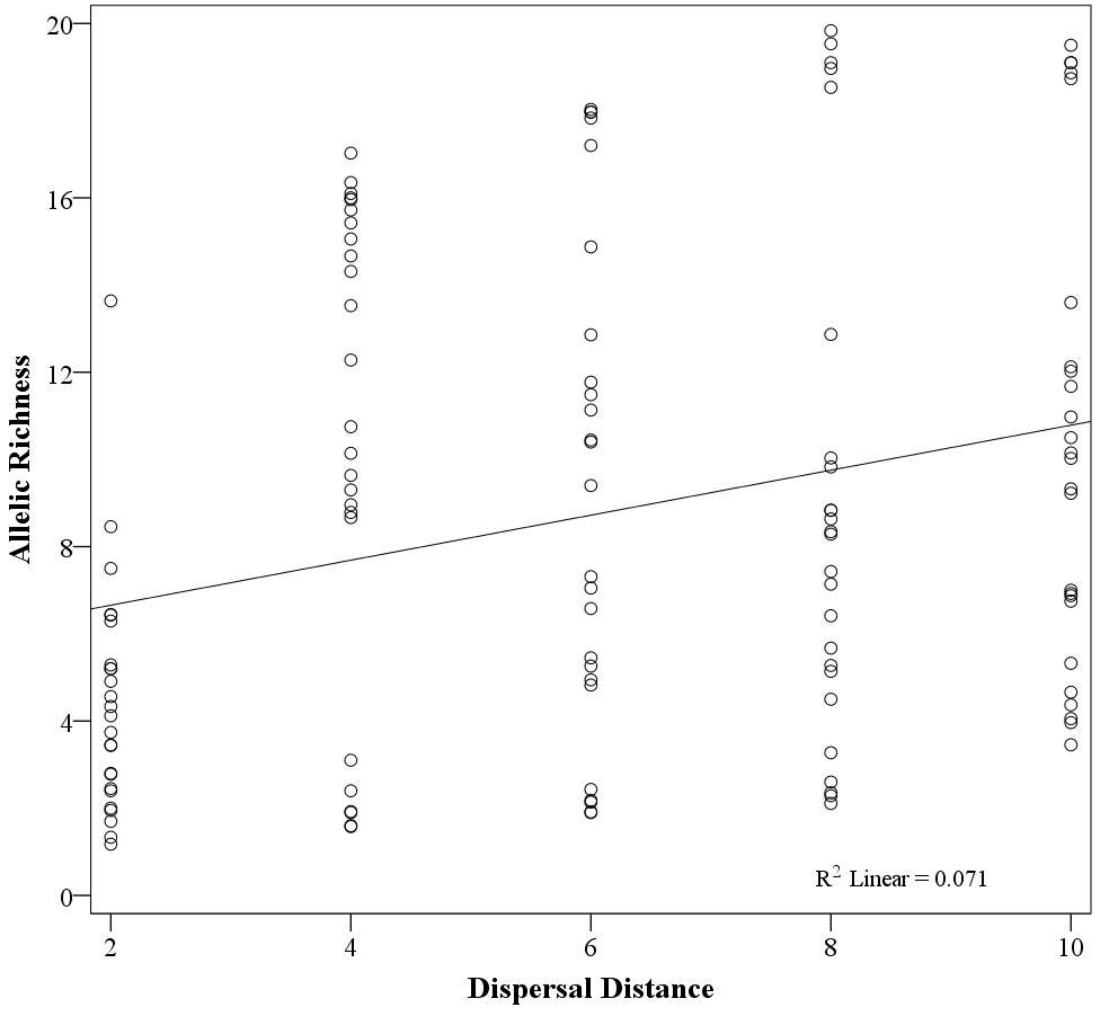

Figure 13 – Allelic richness (A) plotted against dispersal distance (Dav) for 2 year inter-birth interval. R-squared value for 2 year = 0.071.

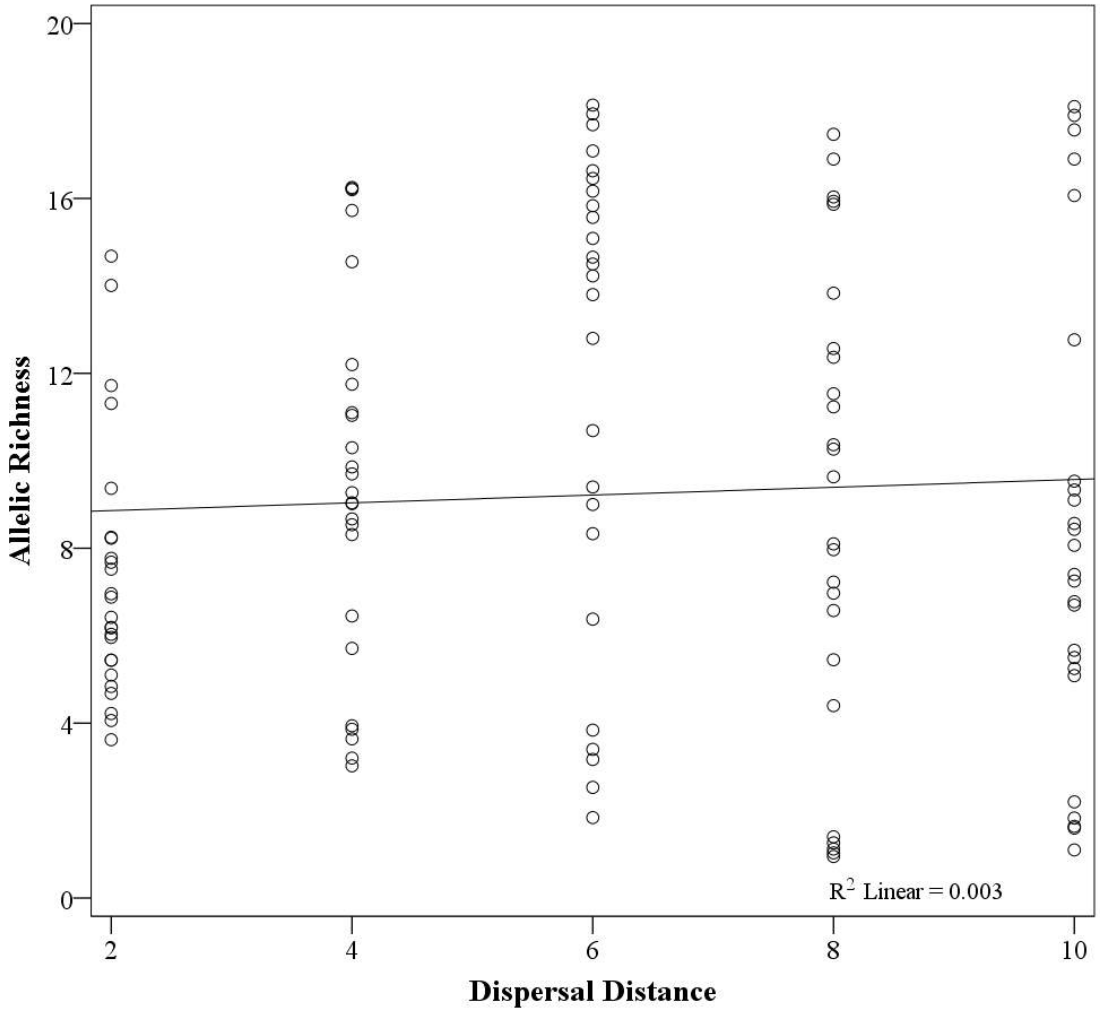

Figure 14 – Allelic richness (A) plotted against dispersal distance (Dav) for 5 year inter-birth interval. R-squared values for 5 year = 0.003.

3.6 *Hypothesis 4 - Life History Traits*

There are many similarities and differences when comparing results from a 2 and 5 year inter-birth interval. *P* had much more of an overall impact on genetic diversity for 2 year, it influenced *A, N* and *He* (figure 1 to 6 and table 1 and 2) when tested with other variables, however, figure 6 suggests that *P* as a single variable had no effect. *P* held much the same effect with a 5 year inter-birth interval except had a greater impact on *N* (table 2). Both inter-birth intervals indicate that *P* has a strong indirect effect on genetic diversity as it was the only variable to significantly impact *N* and *He*; variables used alongside *A* to determine diversity. Similarly, *Dav* only held a significant effect when tested with other variables and only effected *A* when a 2 year interval was used, it also effected *N* and *He* for 5 year, but again, not individually. Although only two results suggest that *H* was a large indicator of *A* (figure 7 to 8 and table 2) for both intervals, it was the only result to have a strong relationship when tested individually against *A* which suggest that this is the strongest direct effector of genetic diversity.

These indirect effects could be the cause of contradictions in data and therefore the variable with the biggest impact towards genetic diversity would be variables which hold an impact individually.

Variables *N* and *He* were dependant on each other during the 2 year inter-birth interval meaning that they and equal level of effect on each other. The same effect is seen with the 5 year interval between *A* and *N*. As these variables are dependent on each other, an indirect effect may be taking place between them which influences the results seen with other variables.

Statistical analysis suggests there is no notable variation in results from 2 and 5 year inter-birth interval, nevertheless, allelic richness was higher in all outcomes with a year interval demonstrating that species with a 5 year interval would be more impacted by the environmental variables. Averages of *A*, *N* and *He* were calculated throughout variables to create a final figure to determine variations in the maximum and average data. The maximum allelic richness for the 2 year results taking into account all variables was 19.833 during minimal fragmentation (0.1) maximum habitat amount (0.9) and *Dav*=8, the maximum for 5 year was 18.133 under the same combination of variables expect for *Dav* which was 6. This is a difference of 1.7 (9%) which is greater than the available allelic richness during some of the results at *P*=0.1, *H*=0.9 and *Dav*=2 and therefore a significant amount. The average *A* was higher in the 5 year inter-birth interval results with a difference between of 0.495 (5%) a fairly significant difference.

Although there was very little difference between *N* and *He* in both sets of results, the small average increase (588/29%) of *N* in the 5 year data could potentially produce results that differ significantly and the level of effect that each variable is holding on the genetic diversity may change due to deviations in other dependant variables. The maximum values of *N* are also suggestively different (1761/59%) between data sets and could hold a similar overall effect on diversity.

The average *He* was slightly increased in the 2 year results by 0.017 (6%) throughout, the difference between the maximum values from both data sets was 0.077 which is an 8% significant deviation when *He* is used to calculate genetic diversity. As heterozygosity was higher on average at the 2 year interval, it is suggested that this variable does have an impact on genetic diversity.

Analysing these slight variations in results as well as statistical analyses results shows the importance of running multiple tests and graphical representation, sometimes even minimal variations can lead to a significant impact. As these results are a representative

fraction of genes and diversity found within wild populations, when approximately scaled to the match wild population genetic diversity, the minimal variation in results become significant. This cannot be overlooked and should be taken into consideration when using models and their results to create hypothesised projections.

4.0 Discussion

Various environmental and biological factors influence changes in genetic diversity, since the aim of this project is to explore the impacts of environmental variables and which factor has the most impact on genetic diversity, fragmentation and habitat amount are discussed. Alongside this, biological traits such as inter-birth interval, life history traits, population size and dispersal distance are discussed as these are also factors which determine genetic variability. Fragmentation held the biggest influence on genetic diversity, whilst the other variables tested (habitat amount, dispersal distance, and population size) held a small level of impact in certain situations. All variables impact each other indirectly when extreme measures of a single variable are tested, however, not all variables impact genetic diversity.

4.1 *Life History Traits*

Heritability is a major factor determining fitness in offspring and survival rates of future generations. The level of heritability differs between populations depending on the active gene pool; life history traits play an influential role on heritability and gene distribution therefore, altering the active gene pool (Reed and Frankham 2003). The active gene pool is a total of all genes within a breeding population;- geriatrics;- individuals too old to breed and those which cannot reproduce (e.g. due to illness, age or lack of available mates) are not included in the active gene pool, therefore, average fitness is lower in populations with a higher abundance of non-breeding individuals. Life history traits differ drastically between primates with some species being comparatively more successful. There is a strong correlation between life history traits and environmental disturbances. Slow reproducers such as *Pan troglodytes* (chimpanzee) suffer more in the long-term with disturbance. The impact on genetic variation at the start of the disturbances will be trivial but gradually increases over time with worsening environmental disruption. More rapid reproducers suffer acute short-term effects and gradually recover over time (Sole et al 2010).

P. troglodytes and *Pan paniscus* (bonobo) are similar in life history traits, both have an approximate inter-birth interval of 3-5 years with first parturition taking place at the age of 12-15 in females. Although males become fertile at the same age as females, they are not classified as adults until they reach the age of 15 or 16 whereas females are adults at 13 (or when the first offspring is born, depending which is sooner). Usually only 1 offspring is born every parturition and it is rare for the species to have 2 offspring (Charnov and Berrigan 2005). The average lifespan of wild *P. troglodytes* and *P. paniscus* populations is

between 40-50 years, females undergo lowering fertility from the age of 30 although they can continue to reproduce past this age (Marchant et al 1998). Taking all these factors into account, females have an average of 4-6 offspring throughout their lifetime, the number of offspring males sire is often unknown as to avoid infanticide and therefore the model replicated this by having males mate with any available female with no copulation interval. The model used 10 years for breeding age as a minimum, but maximum age was lowered to 35 in order to accommodate for increasing infertility with age and as a maximum age for species with a shorter lifespan. Results suggest that longer inter-birth intervals have a weak correlation with genetic diversity. Diversity was lowered by 9% displaying that this variable holds a significant impact, however, average diversity was higher by 5% throughout (excluding the results seen at H=0.9 (figure 10)), indicating that species with an average 5 year inter-birth interval are less tolerant of severe environmental factors than those with shorter inter-birth intervals (like several monkey species).

Some species which have a shorter inter-birth interval include several *Chiropotes* (bearded saki monkey), *Cebus* (capuchin monkey), *Alouatta* (owler monkey) and *Papio* (baboon), species which have intervals between 1-2 years (Peetz 2001). Other life history traits that may alter genetic distribution, such as social structure and life expectancy differ greatly between these species, however, as these were not taken into account in the model, the results can still be applied to the species. Results show that genetic diversity was much more varied at each degree of environmental impact. Similarly to the 5 year interval results, the only outlier was with H=0.9 when diversity reached its peak at 19.81. Average diversity was lower throughout suggesting that species with a 2 year inter-birth interval are much more tolerant of extreme environmental impacts.

Life history traits do impact genetic diversity and often by significant amounts. It was found in this study that inter-birth interval doesn't play a major role in altering genetics, but the minimal impact could gradually worsen and have lasting effects covering both types of species (5 year and 2 year intervals). Other factors such as species tolerance levels and social structure also determine and change how genetic information is distributed throughout populations and should be accounted in situations where models are not used to determine genetic diversity. Ability to survive in damaged habitats changes with differentiation in life history traits. Species with longer inter-birth intervals could be forced to adapt their behaviour in order to survive with these extreme changes as life history traits cannot be changed.

4.2 *Landscape*

Destruction of landscape and habitat is a detrimental factor determining location and arrangement of primate populations. Suitable landscape is required to enable animals to live safely and effectively; disturbances in landscape are known to alter behaviour and specific traits in populations, therefore maintaining size, quality, connectivity and diversity within habitats is fundamental (Anderson et al 2007). Environmental variables such as level of fragmentation and amount of habitat coverage have a prevalent impact on many primates (Marsh 2003) often abstaining to species becoming endangered and heavily threatened with increasing lack of suitable habitat. Often there is a delayed impact of landscape changes. African primates are currently facing threats from historical deforestation and even if populations seem stable, the risk of extinction remains. (Cowlishaw 1999).

Environmental factors are known to impact the composition of populations, when the habitat is severely damaged, species traits may be altered to suit these changes in habitat and can lead to lowered advantageous traits. The tolerance level of these disturbances varies between species, those which are less tolerant are known to suffer with genetic concerns such as; 1) gene flow restrictions; 2) lowered genetic diversity and variability; 3) lowered and lacking advantageous traits; and 4) lowered survival rates and adaptability to changes (Warwick et al 2009, Futuyma and Mayer 1980**).** Differences in biological traits between species and spectrum of environmental impacts on the habitat have an influence on genetic variability, which can either increase or decrease negative impacts mentioned (Hamrich and Godt 1996). Species which are more tolerant to change will also endure the negative impacts that comes with habitat loss and increased fragmentation, this could be a long-term effect and may not always be apparent immediately due to minimal changes occurring over long periods of time (Michalski and Peres 2005). Biological differences and species specific traits such as; 1) diet; 2) dispersal distance; 3) number of offspring per parturition; and 4) social living and interactions, can increase species abilities to cope with extreme levels of fragmentation (Ockinger et al 2010, Hoffman and Willi 2008).

Fragmentation and habitat amount are expected to both have an impact on genetic diversity. Both are widely known to have effects on population size, dispersal and group composition. It is found with many species including certain primates (*Chiropotes satanas and Alouatta*) (Silva and Ferrari 2009, Marsh 2003) that the preferred habitat is that which is more impacted environmentally. It is thought that this could be due to natural or changing social structure (e.g. fewer individuals increases the amount of available

resources available) and those which naturally live in smaller groups (pairs or individually) can thrive in this situation. Using these heavily damaged habitats can also be used as a deterrent against predators or to avoid intraspecific conflicts. As these species can thrive here, it shows that adaptability is higher in some species than others, however, this may not be the best defence against long-term issues such as inbreeding due to isolation (Harcourt and Doherty 2005).

4.2.1 *Fragmentation*

Fragmentation is a major environmental factor which impacts an extensive range of species. The effects of fragmentation are widely studied, its impacts are found to alter species in different ways depending on both species characteristics (e.g. life history traits and behaviour) and landscape characteristics (e.g. size of fragment, diversity in fragments). These characteristics cannot predict if a species will occupy fragments but they do influence species which are already present in the area. Distance of fragments from undisturbed forests is a large predictor of which species may occupy fragments. In a study on primate tolerance to fragmentation by Onderdonk and Chapman (2000) it was found that *Colobus angolensis* (colobus monkey) and *Cercopithecus ascanius* (red-tailed monkey) are more tolerant of fragmentation; *P. troglodytes* and *Procolobus pennantii* (pennant's colobus monkey) are intermediately effected; *Cercopithecus mitis* (blue monkey) and *Lophocebus albigena* (mangabey) have very little tolerance. Those which were more tolerant showed significant difference in behaviour, diet preference, social situation and home range size than those found in undisturbed habitats. Baranga (2004) discovered a similar situation, *Cercopithecus ascanius schmidti* were very tolerant of fragmentation and there was no significant difference between populations which occupied different area of forest and fragments. However, the other tolerant species *Colobus guereza* (Mantled guereza), was restricted in distribution and changes in behaviour were seen.

Fragmentation was a large indicator of allelic richness for both 2 and 5 year inter-birth interval and the difference between 2 and 5 year results was 9%. This is indicative of tolerance level between species with this life history trait. Those with a 2 year inter-birth are more tolerant of high levels of fragmentation and those with a 5 year are less tolerant to the same degree of fragmentation. This correlates with literature and the study by Onderdonk and Chapman (2000). *C. angolensis* have an inter-birth interval which is around 2 years and were found to change their behaviour based on landscape characterists implicating they are more adaptable and tolerant to environmental changes. However, *L. albigena* also have an approximate inter-birth interval of 2 years (Deputte 1991) and was

found that this species has very little tolerance of fragmentation. As these species were located in the same areas during the study (e.g. undergoing the same degree of fragmentation), there is no correlation between inter-birth interval, fragmentation and survival ability. As *L. albigena* remained in the undisturbed habitat, it could mean the species is hit much harder with a larger scale of effects when fragmentation does occur in their habitat. *C. angolensis* is already adapted to some levels of fragmentation through alterations of intraspecific traits which means this species will be less effected long-term and in worsening conditions.

The effects which these species will be facing include, less resources and access to resources (e.g. less suitable habitat, less food sources, isolation). Each impact holds its own effect on genetic variability, for example, isolation leads to lowered genetic drift and therefore metapopulations have a restricted gene pool (Hanski and Gaggiotti 2014). As these impacts are more severe with heightened levels of fragmentation (Kramer et al 2008), less tolerant species and those already suffering are expected to be impacted further and often to the extreme; perhaps leading to such a severe reduction in gene pool size that future generations cannot be supported. This severe reduction in genetic variation can be seen in figures 1 and 5 where allelic richness greatly declines with increasing levels of fragmentation. With reduced richness, there is less genetic variability; if environmental factors remain at the same scale that caused the reductions, gene pool size is likely to be reduced and this is when advantageous traits and adaptability is lost (Vrijenhoek 1998).

4.2.2 *Habitat Amount*

Habitat amount is another key factor which aids in the support and longevity of species within a habitat. Again, tolerance plays a role in determining the length of time species are able to survive in a damaged habitat which is undergoing pressures from size reduction and loss of features. Those with a higher tolerance for such environmental pressures are often referred to as ‘winners’. These ‘winners’ are more capable and adapted to surviving in highly homogenised human-altered environments (McKinney and Lockwood 1999).

Fragmentation and habitat amount influence each other (e.g. fragmentation leads to lack of suitable habitat) which leads to a cumulative effect on species and their genetic diversity. Fragmentation causes habitat loss through anthropogenic interference such as the construction of roads and buildings requires large patches of habitat to be removed in order to have a suitable development area; biological traits can also lead to lack of habitat caused by fragmentation, if the species is unable to travel and disperse between multiple fragments, large portions of the habitat are inaccessible (Fahrig 2003). The cumulative

effect seen is caused by multiple environmental factors having an impact simultaneously pertaining to extreme habitat pressures, which then furthers the rate of impact (Theobald and Hobbs 1997, Robinson et al 1992). Genetic diversity and overall ecosystem diversity is negatively impacted by these cumulative effects, a lack of suitable habitat causes barriers to gene flow and an inability to sufficiently disperse and extend gene variations into other populations (Slatkin 1987). As suitable habitat amount lowers, species are forced to relocate, become isolated or adapt to such changes. All of these factors cause changes in genetics by altering which traits are more desirable (Hanski and Gaggiotti 2014).

Results indicate that habitat amount did not have an impact on the distribution of genes throughout the population making results very varied, however, when tested with other variables, habitat amount held a significant impact. With more habitat coverage, allelic richness was increased in both 5 year and 2 year inter-birth interval results, but was significantly higher in the 2 year results. This suggests that species with a 2 year interval are less impacted by loss of habitat and are therefore the 'winners', however, species with a 5 year interval are impacted and would suffer much more with habitat loss. Both sets of results are highly varied, with more coverage results are very high, with low coverage results are extremely low, offering a huge effect from habitat amount. However, this was only the case when tested with other variables signifying that this has a cumulative and larger scale of effect when other environmental pressures (e.g. fragmentation) are also present.

Dispersal distance and home range are two factors which are dependent on habitat amount. If dispersal distance is larger than the amount of available habitat, then species cannot successfully disperse, consequences and intra-specific conflicts may be increased due to this. Similarly, if species cannot fully disperse, home ranges may begin to overlap and cause further distress on the species (Travis and Dytham 1999, Fahrig 2001). Consequences of habitat loss include heightened aggression between metapopulations; being forced to survive in habitat which is lower in quality due to the inability to disperse further; and a reduction in home range size of met-populations to accommodate for the extreme number of individuals in a small amount of habitat (Hanski 2005). Many primates are vastly territorial (e.g. *Gorilla, Hylobates* (gibbon)); being forced into situations where more individuals are in close proximity will cause an increased number of conflicts over resources which lowers the possibility of gene distribution (Mitani and Rodman 1979, Palombit 1993). Primates which are tolerant of living in smaller home ranges or forming larger social groups (e.g. *Pan and Cebus*) will have a higher rate of survival due to increased adaptability, although resources will become extremely limited (Matthews

2009). Therefore it is vital to conserve as much habitat as possible in order to prevent conflicts and lack of resources to populations which might otherwise be thriving and stable.

4.3 *Population size*

The size of a population is another indicator of genetic diversity. Larger populations are known to have a much varied gene pool whereas smaller populations suffer more from genetic loss. Isolated populations are often small and struggle with lack of gene flow (Rousset 1987). Small populations are likely to have an increased risk of inbreeding which again is another restriction seen to lower diversity and effect survival rates and fitness within a species (Keller and Waller 2002). Although large population sizes increase diversity, they are more likely to be impacted by environmental pressures as resources (e.g. space and food) are shared between more individuals (Shaffer 1981).

Results in this study indicate that population size did not have a significant impact on genetic diversity with outcomes being incredibly varied. Species with a 2 year inter-birth interval had a lot more variation in both allelic richness and population size; 5 year results were more clumped around small population but with very mixed allelic richness. These results suggest that population size, much like habitat amount may hold an indirect effect on genetic diversity with a very weak correlation.

Primates differ greatly in population sizes depending on location, species and social dynamics. As population size impacts the distribution of genetic variation throughout populations, primates in specific circumstances (e.g. those is isolation and those in large and widely dispersed groups) will undergo a greater threat from environmental pressures (Lui et al 2016). It was found in some species such as *P. paniscus* that population size within sexes is altering the distribution of genes. Male scarcity in several metapopulations resulted in only female specific genes and traits being present throughout all observed populations, whereas the male gene dispersal was within populations (Eriksson et al 2006). This suggests that with low population size in either sex, genetic information is not even distributed. Although the model has an approximate equal number of males to females, this cannot explain the results found. However, it does suggest that population size along with dispersal ability and distance may have an impact on genetic diversity, which means population size could again have had an indirect effect in the model giving reason to the results seen.

4.4 *Dispersal Distance*

As individuals disperse, gene flow is increased, therefore dispersal distance plays a role in the dispersion of genes and genetic diversity throughout populations. Both long and short distance dispersal is advantageous for many species in order to disperse varying genes throughout metapopulations; dispersal is also beneficial for biological motives (e.g. territory, survival, finding mates) (Nunn et al 2014). In fragmented environments, dispersal can be limited depending on the rate of fragmentation and distance between fragments. This can lead to metapopulations being isolated which hugely restricts gene flow, this was found in several isolated *Saguinus bicolor* (pied tamarin) populations in Brazil (Farias et al 2015). When gene flow becomes highly restricted, populations begin to lose gene diversity causing homogenous populations to be more prevalent, species survival rates and adaptability will be impacted in this situation. *Trachypithecus leucocephalus* (white-headed langur) are found to be impacted this way, populations monitored were found to have much higher relatedness, with less genetic diversity than other wild populations which were not restricted in gene flow (Weng and Yoa 2017).

In this study, dispersal distance did not have any significant impact on genetic diversity independently and results were varied. However, allelic richness increased as dispersal distance increased which could indicate that dispersal distance had indirect effects due to increasing impacts from environmental factors. When dispersal distance was tested with other variables (fragmentation and habitat amount) results were more linear and when *P* and *H* were minimal (e.g. 0.1 to 0.3), dispersal distance held more of an impact. When tested dependently, no significance was found which indicated that dispersal distance only had an impact when environmental determinants were having an impact on genetic diversity. Genetic diversity may not have been altered, however, the changes seen in allelic richness may have long-term impacts for future generations and could eventually lead to minimal gene flow and disappearance of some traits.

Dispersal aids biodiversity through seed dispersal, primates are one of the most influential species in seed dispersal, therefore their habitat relies on them to disperse suitable distances in order to maintain abundance and diversity of flora (Fuzessy et al 2017). Dispersal distance differs between species, therefore both floral and faunal species which are limited in dispersal will be impacted differently. Species with a greater dispersal distance will have different struggles in damaged and fragmented ecosystems to those with a short dispersal distance. Genus' with a long dispersal distance (e.g. *Hylobates, Pongo*) may find it easier to cross between fragments, however, they may face problems such as

territory overlap, limited food supplies and available mates (Peres et al 2015), which can results in lowered abundance and less gene flow. Genus' with a short dispersal distance such as *Eulemur* (lemur), *Varecia* (lemur) and *Cebinae* (capuchin) will have issues with crossing between fragments and will become isolated much more quickly, but this also means that populations in these fragments can still maintain some genetic diversity through gene flow from metapopulations (Valenta et al 2015, Razafindratsima et al 2013).

4.5 *Genetic diversity*

Maintaining healthy levels of genetic diversity is important not just for species survival, but for overall habitat health, endurance and biodiversity. Genetic diversity can be altered by multiple factors such as; environmental (habitat amount loss, fragmentation); anthropogenic disturbances (urban development, deforestation), life history and biological traits (dispersal ability and inter-birth interval) as well as species specific traits (diet, social living preferences) (Romiguier et al 2014). As genetic diversity can be impacted by the environment as seen in the results from this study, preventing extreme stress on ecosystems from environmental factors is vital in order to protect biodiversity. The effects on genetic diversity which are commonly seen from high levels of fragmentation include; 1) lowered and limited genetic diversity and variation; 2) decreased gene flow; 3) increased inbreeding risk; 4) isolation; 5) speciation; and 6) extinction (Wang et al 2017, Lui et al 2015).

According to the results in this study, certain environmental factors such as fragmentation have a greater impact on genetic diversity, whereas others hold very little effect. In this study, fragmentation was the only environmental factor to independently impact allelic richness. All other factors tested in this study, both environmental and biological (habitat amount, dispersal distance and population size) held the greatest impact on genetic diversity when fragmentation was also present or when two or more variables were present. In many landscapes, multiple environmental and biological factors are present and it is very rare for a habitat to be impacted individually by any of the factors used in this study. This indicates that genetic diversity might not be highly effected unless several factors are present, even at minimal levels of impact (e.g. small urban developments on the outskirts of a habitat), when more than one factor is effective at the same time, impacts to genetic diversity and variation will be seen. However, this does not mean that severe levels of one variable will have no impact, it will still hold an impact but the habitat and species may be more tolerant to certain factors such as population declines and limited dispersal distance. For example, species which are threatened with extreme levels of one factor (e.g.

habitat loss), may not be as impacted as species which are impacted by several low level factors.

4.6 *Wider impacts*

As primates are keystone species (Mills et al 1993), many other species are dependent on them to maintain ecological balance in the habitat and ensure diversity. When ecosystems begin to suffer due to environmental variability, species within that habitat are also impacted. Due to inhabiting fragile and often disturbed habitats, primates are one of the biggest suffers when it comes to environmental impacts. If impacts (loss of habitat and fragmentation) become too extreme, biodiversity throughout varying ecosystems will suffer (Pimm et al 2014).

There is a wide range of evidence that suggests primates are one of the largest seed disperses in forest habitats (Heymann et al 2017, Bufalo et al 2016, Chancellor et al 2016). Seeds which are dispersed by primates provide nesting areas for birds and other animals, food for a wide variety of species including the primates themselves and helps to maintain diversity of both flora and fauna within the habitat (Luna Gabriela de 2016**).** Therefore if primates are suffering from population size crashes, reduced dispersal distance and limited gene flow, their abundance and diversity will begin to lower which will, in turn, have impacts for the whole ecosystem, putting not only themselves but a variety of other species at risk of diversity loss**.**

5.0 Summary and Conclusions

Fragmentation concluded to be the main environmental factor in altering genetic diversity through lowering allelic richness and cause a large variation in heterozygosity. At extreme rates of fragmentation, genetic diversity was highly varied, it caused a linear decline in heterozygosity and allelic richness at different scales. With many habitats currently threatened by fragmentation, various taxa are impacted by lowering genetic diversity which leads to problematic situations such as; 1) lowered advantageous traits; 2) less adaptability; 3) increased mutation risk; 4) increased inbreeding rates; 5) isolation; 6) speciation and; 7) extinction.

Reductions in habitat amount held very little impact on changes seen in genetic diversity in this study, however, since lowered habitat amount is a secondary effect caused by fragmentation, these two variables are linked. Lowering habitat availability and size caused unwanted situations for many taxa such as; 1) lowered dispersal distance and ability; 2) isolation; 3) increased territoriality and; 4) reduced gene flow. Removal of large habitat patches in the same location will hold little impact, but when large scale destruction takes places in several locations within the habitat, genetic diversity will be lowered creating more homozygous populations. Similarly, population size was not significantly impacted by environmental factors and it did not hold an impact of genetic diversity. However, when more than one tested factor in this study was present, population size was highly varied which can cause similar issues to loss of habitat.

Biological factors such as dispersal distance and inter-birth interval were also tested in this study, it concluded that dispersal distance did not have a significant impact on genetic diversity. However, large variations were seen in allelic richness and heterozygosity between 2 and 5 year inter-birth intervals. Changing dispersal distances are dependent on both environmental factors and species characteristics, but dispersal distance does not directly impact genetic diversity. The results in this study from 2 and 5 year inter-birth intervals are similar. However, species with a 2 year interval begin to see impacts to their genetic diversity at increased rates of environmental and biological impacts, whereas, species with a 5 year interval begin to see genetic changes at much lower factor levels. The biological factors in this study are also impacted by behaviour, individual size, population size, species interactions and diet; since these are species dependant factors, genetic diversity will be impacted in a wide variety of ways throughout species, individuals and populations depending on these traits.

Tolerance and species adaptability also play a role in determining the distribution of genetic diversity throughout populations. Many species are found to have little tolerance towards environmental impacts, however, some species express high levels of adaptability to certain situations. Taking this and the results seen in this study into account, it can be estimated with primates which species will suffer greatly from increasing environmental pressures and in which ways they will suffer. Genetic diversity can be used to understand species specific traits and requirements and therefore this information is best used to inform management and understand how species may have previously been impacted by changing environments.

To conclude, environmental factors have various scales of impact on genetic diversity depending on the species biological traits and the scale at which the factor is impacting the habitat. Species specific traits and requirements also play a key role in how genetic diversity will be impacted and how tolerant the species is to the effects of the environmental changes. Monitoring changes is genetic diversity and understanding how environmental, anthropogenic and biological factors impact these changes is important for informing conservation, as without it, conservation cannot be fully effective. As many primates have previously or are currently impacted by variable environmental stress and as many species are important in maintain diversity throughout ecosystems, it is vital for genetic information to be understood. Using models to aid in determining changes in genetic diversity which may be found in wild populations prevents conservation management having little effect long-term and focus can be placed on preserving both ecosystems and individual species genetic diversity. Although environmental impacts are the focus of many ecological studies, genetic diversity and variability are important in determining the scale of impact management will have and will encourage conservation efforts to be placed on species which are not as tolerant and adaptable to change or that are already severely threatened with genetic diversity loss and habitat destruction.

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Appendix I

Evaluative supplement

Originally, the study was going to involve behavioural observations of primates at a zoo in the UK which involved studying changes in behaviour to feeding times alterations. Many zoos did not respond when contacted which left very little time left to undertake the study. In the end these study plans could not take place due to lack of available funding to warrant the zoo visit and lack of time. From this came another study involving zoos. The new project idea was to create a database of various primate foot and hand prints and analyse a selection of these for similarities and differences in order to provide data on foot and hand print evolution for Dr. Matthew Bennet. After re-contacting several zoological societies around the UK, many of them rejected the project idea which then lead to it being abandoned. Time was also an issue here as it was a concern as to how long it would take to create the database with the time that was available.

After these initial failures, it was agreed with the project supervisor that a desk study would be the best option to proceed with as time was quickly running out. After a study was decided upon, there was one final limitation to overcome. At first, the project was to analyse genetic variation between metapopulation of *Pan. troglodytes*, however, since modelling is a new skill gained throughout this project, the idea had to be altered to create a much simpler version of the intended model. After discussion with the supervisor, the idea to create metapopulations within the model was not viable in the time frame so to accommodate this the model was altered to provide data for one large population instead.

There are many strengths and weaknesses involved in this project. The main strength being the efficient data collection methods. After the model was adapted to fit the purpose of the study, data collection took approximately 5 days which is substantially less time than a field or observational study. Another strength is the utilisation of an already established and recommended model, this means very little issues with the validity of the data as the model has been previously used for many other similar studies. Additionally, the study provided a further understanding of genetic issues surrounding environmental impacts and enhanced the results from previous similar studies.

However, this does not mean the project was without limitations during the study process. The biggest limitation to this study was time constraints. Many models take months to develop and unfortunately, after the initial problems with projects being abandoned, time was extremely limited and therefore a simpler version of the model had to be used. At the start of the project, a very little understanding and experience of models was present,

therefore, this was another huge limitation as a whole new method of data collection needed to be learnt. Learning modelling, coding and computer language proved very difficult whilst undertaking other projects and staying on track with this study simultaneously. Another limitation was the limited literature and resources available surrounding modelling using Netlogo, only 2 books were found to be useful and meetings with a PhD student had to take place to get a grasp of the software.

Although these multiple very limiting downsides of the project may seem to impact the quality of work, there is still a potential for this study to be useful for future research and work. As previously stated, the model could be further enhanced to analyse metapopulations which would offer different results but the study premise would be similar. This results of this study provide a base knowledge on the effects of environmental variables and how these may impact species genetics, specifically primates. Related studies have taken place, however, this exact idea has not previously been studied, therefore provides a first for further study. This study can speculate the fate of species when anthropogenic disturbance and plans are taking place, shedding light on species which will require more conservation attention; and providing genetic results before difficult and time consuming in-field studies take place to monitor environmental effects.

From this project, its limitations and mishaps, I have learnt a great deal about my capabilities and time management. Netlogo, modelling and coding was all new to be before starting this project, throughout the time of this study I have successfully learnt a great deal about these and now feel confident using Netlogo in the future. This also tested the scope of my abilities; I was unable to finish the intended model in time due to lack of understanding and time constraints. This has shown me that I had already learnt a great deal and knew that I wasn't going to be able to complete the model. This study has taught me how to better manage my time, from the start of the project I was behind several of my peers due to the number of limitations and project failures I had. However, with careful time management after these issues, I was able to get back on track and there was no need to rush anything which increased the quality of my work. One of the main things I have taken from this project is the further understanding on the topic at hand, previously I knew very little about the topic and chose to study it out of interest, I am now much more aware of the issues surrounding genetic variability and how environmental variables impact species differently.

I have also gained and enhanced several skills due to this project, the most important is my academic and scientific writing skills. This has improved dramatically throughout this project due to having control of my own work and flexibility of my goals. Another

important skill which I have enhanced during this project is the utilisation of SPSS. I have discovered many additional features of this programme and I feel I am now efficient and professional with its use.

Overall, this project has taught me many valuable and important skills required within the scientific community. Learning a whole new programme and how to efficiently use it is the biggest accomplishment of this study and I feel this skill will come in much use in the future. Since several of the original study plans fell through, I now know to take control of situations like this before time becomes limited and I have to forfeit parts of a project to accommodate for these kinds of issues.

Appendix II

Interim feedback

Student Research Project Interview – Agreed Comments Form

Student Name: Abby Pidgen	Programme: Ecology and Wildlife Conservation
Date: November 2016	IRP
Supervisor Name: Amanda Korstjens	

Abby has worked very hardbut she has had several set backs as we changed the topic twice before and during the summer. In the end she started fresh after summer with a very difficult topic.
For this she had to learn modelling in netlogo but she wanted to work on the effects of fragmentation on genetic variability and a model was the only way we could do this.

I am very impressed with her resilience and hard work. It would be good to ensure you come to see me any time you struggle.

Abby presented her work as part of the interim interview to a group of PGRs and staff in the 'Creature Comforts' group meeting. The presentation was very good and clear.
Feedback and comments were provided by the audience at the end of the presentation.

Most importantly for moving forward we discused to get her introduction to me before Christmas and to try to complete the model in January so it does not take away from her write-up time.

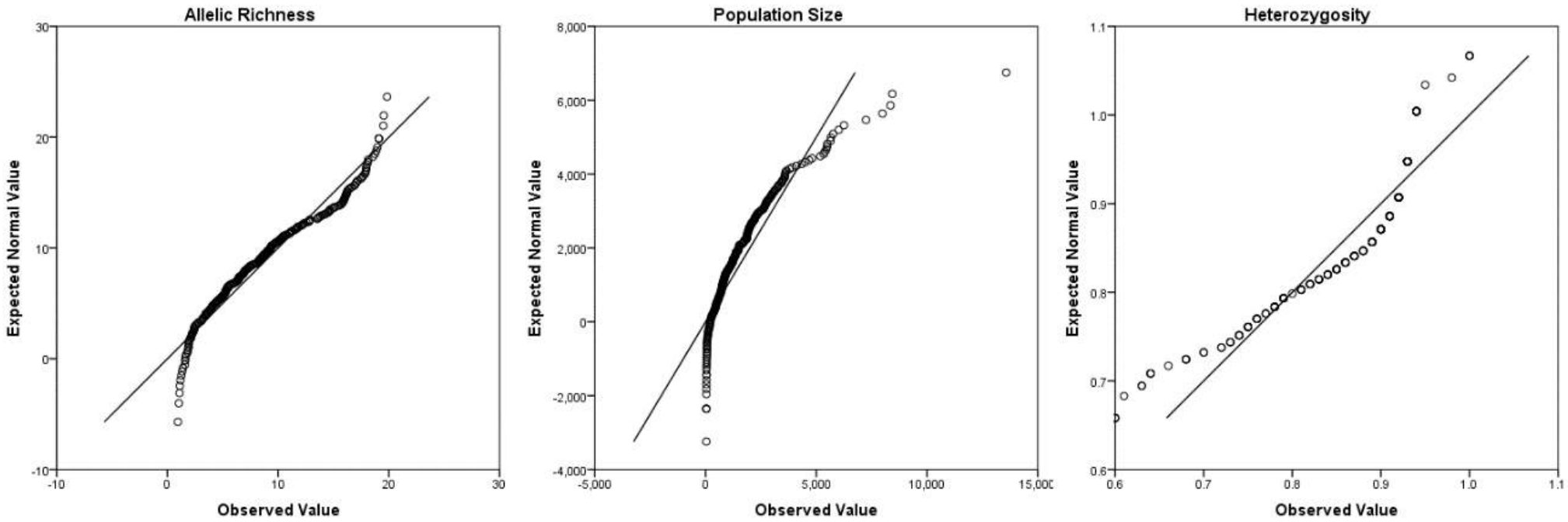
Overall, I am sure that Abby will competently complete her dissertation on time.

Two copies of this form are needed – student to retain one copy the other is to be handed in to the student admin office C237.

Student Signature: Abby Pidgen	Supervisor Signature: Amanda Korstjens

Appendix III

Q-Q plots



Appendix Figure 1 - Q-Q plots indicating normality/non-normality within allelic richness (A), population size (N) and heterozygosity (He) data.