

Comparing the Rates of Adaptive Change in Species Across Biogeographic Gradients

by

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A thesis submitted to the Department of Biological Sciences, University of Manitoba,

in partial fulfilment of the requirements for the course

BIOL 4100 (Honours Thesis)

for the degree of

Bachelor of Science (Honours)

@April, 2023

Abstract

The process of adaptive evolution allows a species to persist with specific traits tailored to their environment. The rate at which a population adapts can change based on the varying environmental abiotic and biotic factors of their location. Environmental characteristics such as the amount of available energy, elevation, temperature and degree of human disturbance thus affect the rates of adaptive evolution across biogeographic gradients. In this study, I used data on adaptive rates for terrestrial species and aimed to determine if the rates of adaptive evolution showed patterns related to spatial biogeographic patterns and environmental factors such as elevation, evapotranspiration, precipitation and temperature. Additionally, I tested whether the rates of adaptation changed based on these specific environmental factors and a human density. The results of my data analysis detected that the rates of adaptation showed good variation in relation to spatial scale patterning but no significant correlation patterns between the tested environmental variables and the rates of adaptive evolution were detected. This result did not support my hypothesis that the rates of adaptive change would vary through space with environmental gradients. Many potential factors may have caused this inconclusive result. Further research into this topic would be useful to understand and predict the adaptive evolution of species' in varying environmental gradients. I propose that studies on this data should aim to utilize more of the available samples within this public dataset such as the aquatic species. Additionally, further research may benefit from narrowing the study size based on location or taxa for significant relationships to be accurately detected.

Acknowledgements

I would like to recognize the many members of the Population Ecology and Evolutionary Genetics Group at the University of Manitoba, who assisted my thesis data analysis. I would like to say a special thank you to my advisor Dr. Colin Garroway and my honours thesis committee members Dr. Kevin Fraser and Dr. Kenneth Jeffries. I would also like to thank Evelien de Greef and Chloe Schmidt for their assistance in this thesis project.

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Introduction

The ability of a species to adapt phenotypically can differ based on the features of their environment. Adaptive evolution of species in natural environments is the unconscious process by which traits that increase reproductive success increase in frequency due to natural selection. Generally, individuals that are equipped for the conditions of their environment will have a higher fitness than others ensuring higher survival rates for themselves and their offspring (Orr. 2009). This process in every natural system varies in magnitude and direction of adaptive evolution throughout different environments (Hendry et al. 2008).

As adaptive evolution is based on environmental factors, populations in varying environments have different rates of adaptation, ranging from slow to “rapid” (Sanderson et al. 2021). In cases of rapid evolutionary adaptation, the specific features that a species endures can intensify the selective direction of phenotypic changes for survival. For example, a drastic shift in favour of individuals with larger beaks was seen in Galapagos Finches (*Geospiza magnirostris*) during periods of harsh weather conditions, that limited food supply to large seeds that were only breakable by birds with a large beak phenotype (Grant and Grant, 2006). This case of microevolution across a generation, re-defined which phenotypes were of a higher fitness in this environment, altering the flow of genes passed to further generations. Understanding how species will adapt based on their environment is crucial to predicting how global change will impact populations in the future (Szűcs et al. 2017).

Currently, most studies of adaptive change rely on estimating rates of phenotypic change. Such research is laborious as adaptive change is the result of complex genetic and

environmental selective pressures. As a result, most work in this area is on single species measured through time and in single environments. These single-species studies are necessary to determine the relevance of a species' relationship to its phenotypic adaptations but it has been difficult to synthetically understand adaptive change across taxa and environments.

Phenotype based estimates of rates of adaptive change among species were recently harvested from these single-species studies and compiled in a public database titled the "Phenotypic Rates of Change Evolutionary and Ecological Database (PROCEED)" (Gotanda & Gorné, 2023). These data span two decades of work and contain 7338 standardized and georeferenced estimates of adaptive change from around the world (Sanderson et al. 2021). Using this data collection, my aim was to analyze and compare the phenotypic rates of change of species across varying environmental biogeographic gradients.

The continuous combined phenotypic and behavioural adaptations of a species is termed "contemporary evolution", as "rapid evolution" can only be used when specific rates of evolution are confirmed as comparatively fast (Sanderson et al. 2021). Understanding how biogeographic gradients such as human disturbance, energy availability, elevation and temperature described in detail below, affect phenotypic adaptation rates can provide insight into how contemporary evolution can be correlated with environments. These data provide a means for researchers to confidently predict how a species with an unknown rate of adaptation will phenotypically evolve in a specific environment.

Human Disturbance

The role of human disturbance in environments has been shown to change the direction and intensity of species' adaptive change. Humans impact natural environments mainly through predation, habitat disruption or fragmentation. Human disturbance can cause significant changes to the previous state of an environment, elevating stressors on species, potentially leading to population decline or extinction in extreme cases (Crispo et al. 2010). For example, an estimated 60% of vertebrate populations were shown to decrease from 1970 to 2014 due to anthropogenic landscape change (WWF, 2018). The fragmented landscapes of cities alter the natural makeup of environments, causing species in these regions to accelerate their rate of phenotypic change (Alberti et al. 2016).

To maintain optimal fitness, species must adapt at faster rates to keep up with the pace of current environmental change. Human predation and disturbance can create an imbalance within natural food web dynamics influencing behavioural and morphological adaptations of populations. It was shown that human supplemental feeding of European Black Caps (*Sylvia atricapilla*) within previously natural environments caused a behavioural change in migration patterns and body morphology (Berthold et al. 1992). Alternatively, morphological changes can occur due to human overexploitation of particular populations and the targeting of individuals of specific phenotypes, causing rapid shifts in selective pressures for phenotypes better suited to avoid predation (Darimont et al. 2008).

Anthropogenic stressors are accelerating and are unevenly distributed across biogeographic gradients around the world. This makes it difficult to accurately measure the rates of adaptation in response to human disturbance and natural variation. I will look

at the rates of adaptive change across spatial gradients of human disturbance, to infer the strength of adaptive signals this imposes on different species. My aim was to analyze the direct effects of human disturbance on adaptive rates such as human population density per square kilometer in comparison to indirect effects such as climate change. I hoped to utilize the disturbance type descriptions provided for each sample in the database to compare how the adaptive rates differed based on the type of anthropogenic influence involved.

Energy Availability

The amount of usable energy within an environment is influential to species richness. When solar energy is introduced into an ecosystem, the magnitude of primary productivity influences the species diversity within the environment (Oindo, 2008). Species diversity within an environment can indicate adaptive levels, necessary to predict the behaviour of phenotypic changes occurring in individuals within these areas. There is a quadratic relationship between species richness and productivity within an environment as diversity increases in periods of low productivity and declines in times of high productivity (Oindo, 2008). This relationship can be used to predict the rates of adaptation in varying gradients of energy availability. The rates of adaptation should be highest in geographic areas of low energy availability. I will determine whether adaptive evolution rates follow a quadratic relationship with the available energy of the environment. Quantification of energy availability will be measured by the levels of energy transfer through an ecosystem. Environmental factors such as precipitation and evapotranspiration

rates will indicate the rate of energy movement into, throughout and out of an ecosystem (Katul et al. 2012).

Elevation

Elevation can impose unique selection pressures for populations inhabiting moderate to extreme elevational regions. Generally, areas of extreme elevation provide unfavorable environmental features that challenge species living within them in comparison to moderate and low elevations. For example, species adapted to live in high elevations must endure cold temperatures, high UV radiation levels and low oxygen availability (Sun et al. 2018). For a species to survive such extreme conditions, efficient and potentially fast adaptive capabilities are needed while maintaining sufficient fitness. Studies on deer mice (*Peromyscus maniculatus*) inhabiting high and lowland environments have shown changes in their metabolic capacity in response to the varying oxygen availability at different elevations (Storz et al. 2019). Studies such as these have shown the potential for strong adaptive signals in locations with extreme elevations. I predict that the adaptive evolutionary rates of species in our study will exhibit a positive correlation, increasing as elevation becomes greater. High elevations will be relative to the degree of other samples and will be considered based on the gradient scale.

Temperature

Similar to elevation, environmental temperatures exist in extreme gradients impacting phenotypic adaptation in species. These two environmental features relate to

one another closely but may show different patterns of adaptive signaling worth exploring. As temperatures range from low to high extremes, the physiological traits of species must be altered to enhance fitness in these environments. Adaptations of metabolic activity in extreme environments promote metabolic efficiencies such as avoiding water loss through freezing or transpiration. Other adaptations alter the metabolic strategies by which internal body temperature is acquired and regulated. I believe geographic locations at varying points along the temperature spectrum will produce strong adaptive signals. The degree to which these adaptive signals affect different species with varying means of acquiring and maintaining their body temperatures may also differ. I predict that the relationship between the adaptive rates of species and environmental temperature will be quadratic, with high rates of adaptation seen when species are located in very cold or very warm environments and lowering in median temperatures.

Analysis of how biotic and abiotic environmental factors, of natural or unnatural origins, impact adaptive rates, will show the magnitude of each selective pressure. In this study, I aimed to emphasize the magnitude of anthropogenic influence (human disturbance) on the rates of adaptation. I predicted that human disturbance would cause increased rates of adaptive evolution, but I was unsure whether anthropogenic influence would impose a higher magnitude of adaptive signals compared to other environmental conditions as humans indirectly are changing environments through climate change and landscape fragmentation. Alternatively, environments with high human disturbance levels may show a shift in species abundance and community composition of the animal populations in the area. In this case, the adaptive signals of species may be lower in areas of dense human populations.

I will analyze environmental variable and human disturbance values separately however it should be noted that indirect anthropogenic consequences like climate change, constantly affect biogeographic gradients such as temperature levels. This makes predicting biogeographic adaptive rate patterns increasingly difficult in relation to anthropogenic influence. A representation showing the correlation between human disturbance and adaptive rates, especially in comparison to other influential conditions, will allow us to predict the evolutionary behaviour of species. Such predictions could be used in conservatory research and prevention of species decline in anthropogenic environments.

My thesis is that rates of adaptive change will vary through space with environmental gradients. Globally, every geographic area contains varying degrees of environmental conditions, making the quantification of these features difficult. In this study, I used the biogeographic gradient of elevation, energy availability, temperature and human disturbance to predict how different combinations of these features would influence adaptive signals. I predicted that these environment features would correlate with rates of adaptive change. Additionally, I predicted an influence of taxa (birds, mammals, herptiles, insects and plants) on how environmental gradients effect adaptive rates.

Materials and Methods

The main objective of my thesis was to map the spatial variation of the rates of adaptive change provided by the PROCEED database (Gotanda & Gorné, 2023). This public database is a compilation of data from studies used to determine phenotypic rates of change and contains information including species name, taxonomic groups, study

identification numbers, sex, coordinate location, data type (ratio or interval), environmental disturbances, values to calculate adaptive rates, study source and what was measured for each sample. All data analysis in this study was done using the statistical data software program R. The PROCEED database is an on-going resource with researchers periodically adding samples, sometimes with empty variables. To account for this, I manually edited an updated version of the data, removing individual samples without valid location coordinates or adaptive change variables. To properly understand the dataset, I summarized the main categories that could be used to organize the samples and listed them based on taxa (Table 1), species (Table A1) and drivers of adaptive change (Table 2).

Data analysis for specific environmental factors was done using the SDM predictors package in R (Bosch et al. 2022) to pull specific environmental layer information from each sample's location provided in the PROCEED dataset. The environmental layer information included elevation values, annual potential evapotranspiration, annual mean temperature and precipitation. I used the average precipitation and annual potential evapotranspiration environmental layers to assess the energy flow into and out of an ecosystem respectively to represent the energy availabilities of these locations. I extracted the degree of human density per square kilometer values at 0.5 degrees provided by the NASA website as a variable to test human influence (NEO, 2022). These layers connected the dataset samples to their georeferenced environments and allowed me to see the environmental gradient variability.

To make the environmental layer data more representative of the area surrounding the coordinate point of each sample, I added three separate distance buffers of 10 square km, 25 square km and 50 square km. This provided the averaged environmental data from

each location to better represent the features of the whole region. These buffer values were chosen as any value above 50 square km would be too broad to accurately measure the specific sampled environment. I then mapped each environmental variable against the three distance buffers to visualize the location data and the differences between each buffer value.

Each layer in the SDM predictors package is specific and may not apply accurately to every environment. This means that the necessary layer that must be used to extract environmental data can change based on the environmental traits of the sampled individual. The PROCEED database contains samples from terrestrial and aquatic locations. This factor changes the environmental layers that would need to be used to extract aquatic environments compared to terrestrial locations. During analysis of all data points, many aquatic samples were not included in representative figures due to lack of necessary layer data. For example, the average temperature environmental layer did not extract from aquatic data samples properly; the proper layer that would be needed to extract this environmental data would likely need to be a form of the average water surface temperature. This issue could be solved by analyzing the aquatic and terrestrial data samples separately, but for the purpose of this study, I chose to limit my data analysis to terrestrial samples only, removing aquatic data.

To calculate the rates of adaptive change in each sample, I first separated the dataset values based on their data scale. Adaptive data is all measured on a constant interval scale with an exact zero for ratio data and an arbitrary zero for interval data values. It is necessary to calculate the adaptive rates of change for ratio and interval scale data separately because of their statistical differences. I measured the rates of adaptive change first by calculating Darwins for each of the ratio data scale values. Darwins are

defined as the mean proportional change in trait value over one million years (Sanderson et al. 2021), and was calculated as:

$$D = \frac{\ln(\bar{x}_2) - \ln(\bar{x}_1)}{10^6 \text{years}}$$

X1 and X2 are the mean trait values of a population at times 1 and 2, or two populations both known to have a common ancestor. The denominator is set to ten million years as a time scale rate (Sanderson et al. 2021). The rates of adaptive change for data on an interval scale were measured using Haldanes. Haldanes are defined as the mean trait change in terms of standard deviation values in each generation (Sanderson et al. 2021), and were calculated as:

$$H = \frac{\left(\frac{\bar{x}_2}{SD_P}\right) - \left(\frac{\bar{x}_1}{SD_P}\right)}{g}$$

Where g is generation time, the time passed divided by the amount of time in each generation (Sanderson et al. 2021). SD_P is the pooled standard deviation of two samples and was calculated as:

$$SD_P = \frac{\sqrt{SD_1^2 + SD_2^2}}{2}$$

Where SD_1 and SD_2 were the standard deviations of the sampled population at times one and two. Sixteen samples in the database were marked as “unknown” for their

data scale. I calculated the adaptive rates of change for these unknown samples using Darwins and Haldanes.

Using the calculated rates of adaptive change for each sample, the data was input into Moran's eigenvector maps (MEM) code in R. MEM detects spatial patterns in the adaptive rates and displays the degree of these relationships on a gradient scale. This analyzed the rates of adaptive change against the coordinate locations and plotted the spatial patterns on a global spatial scale. Non-spatial and local patterns in the data were ignored. This analysis produced a map displaying the gradient of spatial scale variation seen in the adaptive rates (Figure 3).

The final component of my data analysis was to test the environmental causes of adaptive rate variation and see which of the pre-determined environmental features showed stronger adaptive signals influencing rates of adaptive change more than others. This was done using linear models to detect relationships between the environmental variables and the adaptive rates. The dependent variable was the rate of evolutionary change and each environmental variable was fitted in a separate model. As many of the adaptive rates originated from the same species sample, I used the average value for each environmental variable and adaptive rate for the modelling. For each analysis, I ran a linear model and a logarithmic model. I first modelled all taxa together into one model (Table 3), then I separated the taxa into their own models to detect patterns that may be on a taxa or species level (Table 4). A separate model was fitted for mammals, plants, insects, birds and herptiles in the dataset such as amphibians, reptiles, turtles and snakes. Herptiles were grouped together into one model. I calculated a 95% confidence interval for each estimate's standard error produced from the models.

To detect any additional patterns in my dataset, I produced a correlation matrix between the environmental variables and the adaptive rates (Figure 4). This visual showed the degree of each variable's correlation coefficient related to one another.

Results

The PROCEED version 5.0 database originally contained 7338 standardized and georeferenced estimates of adaptive change. After manually editing the data by removing aquatic species and samples lacking coordinates or adaptive rate variables, the remaining dataset held 3216 estimates for 173 species (Table A1) within 8 taxonomic groups. The largest taxon in the database was birds 1096 estimates of adaptive change; the second largest taxon was insects with 1017 estimates (Table 1).

Each study comprising the database reported the cause of adaptive change for their data. This was determined based on what each entry was studying and the environment before and after the disturbance of interest (Sanderson et al. 2021). The main driver of adaptive change in the database with 1656 samples was from self-induced (natural migration) and post disturbance range expansion (Table 2). Other drivers of adaptive change included introduction of species into non-native habitats, in situ natural variation, climate change, human harvesting, pollution and landscape change.

The results from extracting environmental data using the SDM predictors package are visualized in Figure 1. Each point in Figure 1 represents one or more samples from within the PROCEED database and scales the environmental information on a gradient to compare the differences between each estimate at a buffer of 50 square km from the sample point. Very minor differences in the extracted environmental data occur between the 10 square km and the 25 square km distance buffers. A more pronounced difference

occurs between the 10 square km and 50 square km distance buffers. As the 50 square km buffer is more representative of the average environmental data of each sample's location, I used this buffer to produce an accurate representation of the results. This analysis showed that there is good environmental variability present in the dataset enough to display trends that can vary across biogeographic gradients.

The results of the MEM map display spatial patterns detected in the calculated adaptive rates of change across the global gradient (Figure 3). High levels of spatial patterning can be seen mainly in North America along the west and east coasts, with low levels of spatial patterning occurring in all other continental regions of the globe. This showed high levels of variability of which the adaptive rates were related to spatial scale patterning.

The results of the linear models for each environmental variable against the adaptive rates across all taxa showed no significant patterns. The estimate effect sizes produced from the models were small due to the scale of adaptive rates being millions of years. Each estimate would be considered a significant effect if it overlapped zero when adding or subtracting its calculated 95% confidence interval value. No detectable effects were found from the results of the models for all taxa (Table 3). The results of the separate taxa models showed no detectable effects, similar to the results of the cumulative analysis (Table 4).

The results of the correlation matrix for all taxa showed very little correlational patterning between the rates of adaptation and the environmental variables. This further shows that no significant effects were detected in the dataset values and the extracted environmental information. A strongly positive correlation of approximately 0.8 was detected between temperature and evapotranspiration. The degree of correlation between

human density and temperature was approximately 0.3 and -0.3 for altitude.

Evapotranspiration was correlated to altitude with an approximate 0.2 degree.

Discussion

The phenotype of each individual is heavily specialized to their environment to allow them to have the best possible fitness. The selective pressures that influence the phenotypes of individuals are thus influenced by their environment. Studies on the adaptive phenotypic rate of change seen within populations of a species have aimed to determine what factors can affect the direction and intensity of this process. Previously, it was thought that adaptive change only occurred slowly over many generations, however many natural systems have shown “rapid” rates of adaptation to be common (Kinnison & Hendry 2001) and these rates could be due to environmental effects. I hypothesized that rates of adaptive change would correlate to biogeographic gradients. I predicted that different features across an environmental and human disturbance gradient would correlate with varying rates of adaptive change and that each taxa would each have different responses to these influences. The results showed a strong relationship between the adaptive rates and spatial scale patterning, supporting my predictions. The final result of my study was unpredicted and did not produce significant support for my hypothesis that the adaptive rates would correlate to biogeographic gradients .

The topic of calculating rates of evolution, in this case phenotypic adaptation, has been a field of study for years, largely popular amongst paleontologists (Sanderson et al. 2021). Determining patterns of adaptive change are important to compare the degree of this change across factors of species, taxa or location (Kinnison et al. 1999). It is important to note that my thesis study was based off phenotypic change rather than

evolutionary change however, phenotypic change provides necessary information that can be applied to evolutionary processes (Gotanda et al. 2015).

The results of the MEM map showed that a strong relationship exists between the calculated rates of adaptation and spatial scale patterning across a biogeographic gradient. High levels of spatial scale patterning were detected in North America and may be related to effects specific to the northern or western hemisphere. However, this would not explain the low levels of spatial scale patterning detected in the eastern hemisphere of the globe. I theorize that the lack of spatial scale patterning seen in the eastern and southern parts of map may be due to a lack of sampling in these regions of the world, as many of the estimates provided in the PROCEED database are from North America. Additionally, the high spatial scale patterning in North America may be from specific samples of the same taxonomic group residing in this region. I propose that future studies focus on the samples within North America to better detect the relationships of data with the high spatial scale patterning seen.

The extracted environmental data from each location of the dataset samples had strong variability in the gradients of each variable. The ranges of each variable extended from low to high values, providing enough variation to detect differences in adaptive rates based on these gradients. The results of the linear models for each environmental variable with the rates of adaptation, did not show any significant relationships among all taxa and when each taxa was separated. This means that even though the adaptive rates of change had strong spatial scale patterns across a biogeographic gradient, when looking at the specific environmental information for each location, this was not reflected in the data analysis. This was verified further by the lack of patterns detected by the correlation matrix of each variable in relation to the adaptive rates. Since significant patterns were not

detected between the environmental variables and the adaptive rates, I cannot compare which variables impose greater adaptive signals alone or combined.

As no significant patterns were detected between the relationship of human density and adaptive rates, I cannot predict how human disturbance changes the rates of phenotypic adaptation. The lack of a relationship between human density and adaptive change may be due to my assumption that human density would be correlated with anthropogenic disturbance. If this assumption is not true, this would cause selective signals of densely populated areas not to have a large effect as initially predicted. This lack of a relationship may also be due to a “dilution” effect where significant relationships between human density and adaptive change rates were not seen due to the large sample size. If patterns related to anthropogenic influence had been detected, I planned to compare the drivers of natural adaptive change to the estimates of adaptive change related to human density. I planned to propose theories into how these patterns could predict how large-scale disturbances such as climate change, would be affecting phenotypic adaptation. Although this cannot be done using my data analysis, further research should be conducted to compare the influence of human disturbances on the rates of adaptation in species.

The results of my data analysis did not support my initial hypothesis that the rates of adaptive change would vary across different biogeographic gradients. However, these results impose an interesting question regarding the reasoning for such strong spatial scale gradients within the adaptive rates occurring with little supporting data about the specific environmental conditions from these locations. Currently, my working hypotheses for why this study produced these results are as follows:

1: Genetic Assumptions with Phenotypic Measurements

The data assumes that this evolutionary change is genetic but only measures phenotypes. As stated earlier, the samples collected in the PROCEED dataset were based on phenotypic change rather than evolutionary change. As phenotypes are what is directly interacting with an environment, studies done using this data assume that the phenotypic change are what influences fitness the most (Sanderson et al. 2022). Justifying what is phenotypic versus genotypic when analyzing evolutionary change can be very complex when factoring in all processes influencing selection (Gorne & Diaz 2019). Most studies on adaptive change struggle to distinguish plasticity versus genetic adaptation. For this reason, my analysis may not have produced the expected results due to the adaptive change being assumed as genetic while only considering species' phenotypes.

2: Maladaptive Versus Adaptive Data

The phenotypic adaptive change in my dataset is unclear whether change is adaptive or maladaptive. The samples from the PROCEED dataset were collected based on the phenotypic adaptations of each species. Adaptations are usually thought to follow the selective pressures of a population's environment to better equip the species for survival in that specific environment and increasing their fitness, known as adaptive change. Sometimes the result of random adaptation has fitness costs that outweigh the benefits that this phenotypic trait provides; this is known as maladaptive change. As environments are changing faster in recent years mainly from anthropogenic based reasons such as climate change, their adapted traits can become costly and therefore,

maladaptive. These maladaptive traits are likely to be lost over time as they are not selectively advantageous. The PROCEED dataset does not distinguish whether the change is adaptive or maladaptive and this may be the reasoning that my analyzed environmental variables had no detected effect on the rates of adaptive change.

3: Alternate Environmental Variables

Alternate environmental variables that I did not study could have more of an effect on the rates of adaptation than those chosen in my analysis. I chose to look at five specific variables that I felt would best represent factors influencing changing rates of adaptation in the environments of species. These included potential evapotranspiration, altitude, precipitation, temperature and human density. Future studies on this topic may need to look at other factors within an environment that may show larger effects on the rates of adaptation such as latitude, longitude, topography, vegetative cover, etc. Considering the high levels of spatial scale patterning of the adaptive rates in North America in comparison to the low levels in other areas of the globe, longitude and latitude would be especially useful to study in the future. Based off the strong relationship seen between temperature and evapotranspiration in Figure 4, I believe that these variables are useful and should be looked at further along with new environmental factors.

4: Sample Size and Methods

This type of study may require more estimates of adaptive change or alternate study methods. Although my edited dataset contained 3216 estimates of adaptive change

that I used for my analysis, the original PROCEED data contained over 7000. Future studies done on this topic could utilize the entire database once it is completed and could use both aquatic and terrestrial samples to get a larger sample size that may have more representative results. Additionally, alternative methods of data analysis may provide other perspectives and results that I did not receive from the methods I used in this study. Rather than waiting for the PROCEED dataset to be further completed, I propose further studies utilize the aquatic data that I was unable to, which would expand the available data greatly.

Contrary to this theory, my study may have been too broad to accurately detect significant relationships within the adaptive change data and the corresponding environmental variables. Given the low spatial scale patterning seen in the rates of adaptation in regions of the globe other than North America, a focus may need to be made on a continent wide scale. The unpredicted results of this study could be due to the significant relationships being “diluted” by non-significant data. Reducing the sample size further by a factor of location or taxa may result in a detection of significant relationships in the adaptive rate data with the environmental variables.

5: Random Spatial Scale Patterns

It is possible that the variation seen in the spatial scale patterning of the adaptive rate data is random. The results of my data analysis show high levels of patterning due to spatial scale biogeographic gradients in the adaptive rates of change. It is unlikely, but not impossible that the variation in spatial scale patterning detected is completely random. This would explain why no significant relationships between the environmental variables

and the adaptive rates were detected. However, if this pattern was random, that would not explain why high levels of spatial scale patterning were detected mostly in North America than in other parts of the world. If the patterns were truly random, it would be more likely that the variation in spatial scale values would be seen across the globe. Even in this scenario, the spatial scale patterning could be random and could be the cause for the unpredicted results of this study.

6: Insufficient Time Estimates

The potential inaccuracy of generational and evolutionary time could cause significant bias in the samples. All generational time values were provided in the PROCEED database that I used to calculate the rate of adaptive change. As noted in previous studies, slight inaccuracies of generational and evolutionary time values can cause over or under estimations of evolutionary processes such as selection intensity (Kinnison & Hendry 2001). Additionally, a bias may occur when assuming that small rates of adaptation do not have large evolutionary consequences when passed on to multiple generations (Kinnison & Hendry 2001). Although this theory may have merit, I believe if this was the case, my spatial scale patterning results would not detect strong variability. For this reason, this theory is not well supported by my results.

7: Lack of Data on an Interval Scale

As discussed, the values collected in the PROCEED database were separated into ratio or interval categories based on their statistical differences. This changed how their

adaptive rates were calculated and the units used to measure them. Data on a ratio scale was calculated into units of Darwins and was measured on a large time scale of one million years. Other values on the interval scale, were calculated using Haldanes and were measured using smaller-scale generational timing. Most of the PROCEED database consists of ratio scale data meaning that a large majority of the adaptive rates were measured in Darwins. Contemporary evolution is a rapid process and can cause adaptive change to occur from generation to generation (Sanderson et al. 2021). With this in mind, the unpredicted results of my study may be caused by the large bias towards ratio scale data used to calculate the adaptive rates. Future compilations of adaptive data should incorporate more values on an interval scale to be used to calculate adaptive rates on a generational level.

The reasoning for why high levels of spatial scale patterning gradients in the adaptive rates of change were detected with this not reflected in the specific environments of these locations remain unclear. For this reason, I propose that further studies on how adaptive rates of change are influenced by environmental features and human disturbance should be conducted. I suggest that future researchers expand the basis of this study either by including a wider variety of sample estimates and environmental features or by narrowing the focus of study by location or taxa to detect smaller-scale relationships. Additionally, further studies could aim to distinguish genetic versus phenotypic change in the data to have a higher likelihood of producing the expected results of this thesis.

Conclusion

The results of this thesis did not reflect my initial predictions that environmental gradients would correlate with changing rates of phenotypic adaptation. However, my hypothesis stating that the rates of adaptive change vary through space with environmental gradients, could be further studied and supported in the future. This field of research is important for gaining further understanding of how species populations adapt in a quickly changing world. Anthropogenic influence will continue to change environments around the world and by understanding how this affects the rate of which species adapt, we can predict how species will respond. This type of research will enhance conservation biology efforts by allowing new perspectives and predictions to maintain populations in a constantly changing world.

Tables

Table 1. The number of sample estimates per taxa. Values are from the edited PROCEED version 5.0 database. Estimates without location data or adaptive rate values were removed.

Taxa	# of Sample Estimates
Birds	1096
Insects	1017
Mammals	575
Plants	410
Lizards	74
Amphibians	22
Turtles	21
Snakes	1
Total	3216

Table 2. The frequency of each driver of adaptive change. Values are from the edited PROCEED version 5.0 database. Estimates without location data or adaptive rate values were removed. Range expansion refers to the establishment of a population in a previously unoccupied region either by natural means or by human involvement. In situ natural variation refers to the natural long-term changes of populations. Introduction refers to the transferring of a species into a new environment. Harvesting refers to any case of harvesting or hunting by humans.

Driver of Adaptive Change	Frequency
Range Expansion	1656
Introduction	669
in situ Natural Variation	643
Climate Change	158
Harvest	53
Pollution	36
Landscape Change	1

Table 3. Linear model summaries for all taxa. The linear (lm) and logarithmic (log) model summaries for the averaged data across all taxa samples. A 95% confidence interval was calculated from the standard deviation.

lm Model	Human Density	Temperature	Altitude	Precipitation	Evapotranspiration
Estimate	1.89E-05	4.57E-04	1.71E-07	-2.52E-06	4.12E-06
Standard Error	3.24E-05	3.39E-04	3.33E-06	4.56E-06	6.42E-06
95% Confidence Interval	6.35E-05	6.64E-04	6.53E-06	8.93E-06	1.26E-05
Log Model					
Estimate	-4.18E-03	-5.81E-02	2.01E-04	6.78E-04	-1.46E-03
Standard Error	4.16E-03	4.40E-02	4.05E-04	5.77E-04	8.18E-04
95% Confidence Interval	8.15E-03	8.61E-02	7.94E-04	1.13E-03	1.60E-03

Table 4. Linear model summaries for each taxa separately. The linear (lm) and logarithmic (log) model summaries for each taxa for environmental variables (human density (HD), evapotranspiration (ET), standard deviation (SE)). A 95% confidence interval (CI) was calculated from the standard deviation (SD).

		<u>In Model</u>						<u>Log Model</u>					
		HD	Temperature	Altitude	Precipitation	ET	HD	Temperature	Altitude	Precipitation	ET		
	Estimate	-9.51E-07	-1.02E-05	3.37E-08	-6.60E-08	-9.37E-08	-2.44E-03	-2.60E-02	8.74E-05	-1.67E-04	-2.36E-04		
Mammals	SD	5.79E-07	6.97E-06	5.43E-08	9.49E-08	1.25E-07	1.48E-03	1.78E-02	1.39E-04	2.43E-04	3.19E-04		
	95% CI	1.14E-06	1.37E-05	1.06E-07	1.86E-07	2.44E-07	2.90E-03	3.49E-02	2.72E-04	4.75E-04	6.25E-04		
	Estimate	1.28E-06	-2.33E-06	-4.65E-08	-8.79E-09	8.67E-08	3.21E-03	-1.01E-02	-1.64E-04	7.81E-05	2.86E-04		
Plants	SD	1.19E-06	1.16E-05	1.14E-07	1.03E-07	2.23E-07	3.56E-03	3.43E-02	3.36E-04	3.25E-04	6.57E-04		
	95% CI	2.34E-06	2.27E-05	2.24E-07	2.01E-07	4.36E-07	6.98E-03	6.72E-02	6.59E-04	6.36E-04	1.29E-03		
	Estimate	4.82E-06	1.28E-03	5.74E-06	-1.10E-05	1.25E-05	-4.94E-03	-1.07E-01	1.51E-03	2.08E-03	-4.20E-03		
Birds	SD	9.10E-05	8.63E-04	1.26E-05	1.34E-05	1.97E-05	1.00E-02	8.68E-02	1.30E-03	1.39E-03	1.96E-03		
	95% CI	1.78E-04	1.69E-03	2.47E-05	2.63E-05	3.87E-05	1.96E-02	1.70E-01	2.55E-03	2.73E-03	3.83E-03		
	Estimate	-7.01E-07	-6.82E-07	1.50E-07	1.13E-07	6.70E-08	-8.04E-03	-7.98E-03	1.71E-03	1.28E-03	7.61E-04		
Insects	SD	1.33E-06	9.07E-06	2.05E-07	2.89E-07	1.72E-07	1.53E-02	1.04E-01	2.35E-03	3.31E-03	1.97E-03		
	95% CI	2.61E-06	1.78E-05	4.02E-07	5.66E-07	3.38E-07	2.99E-02	2.03E-01	4.60E-03	6.48E-03	3.87E-03		
	Estimate	1.17E-04	-9.15E-04	-4.58E-05	6.23E-05	-1.40E-05	1.58E-02	1.05E-01	-6.87E-03	8.73E-03	3.03E-03		
Other	SE	9.32E-05	1.34E-03	4.76E-05	3.58E-05	2.21E-05	2.38E-02	3.34E-01	8.63E-03	7.24E-03	5.23E-03		
	95% CI	1.83E-04	2.64E-03	9.34E-05	7.02E-05	4.32E-05	4.66E-02	6.55E-01	1.69E-02	1.42E-02	1.02E-02		

Figures

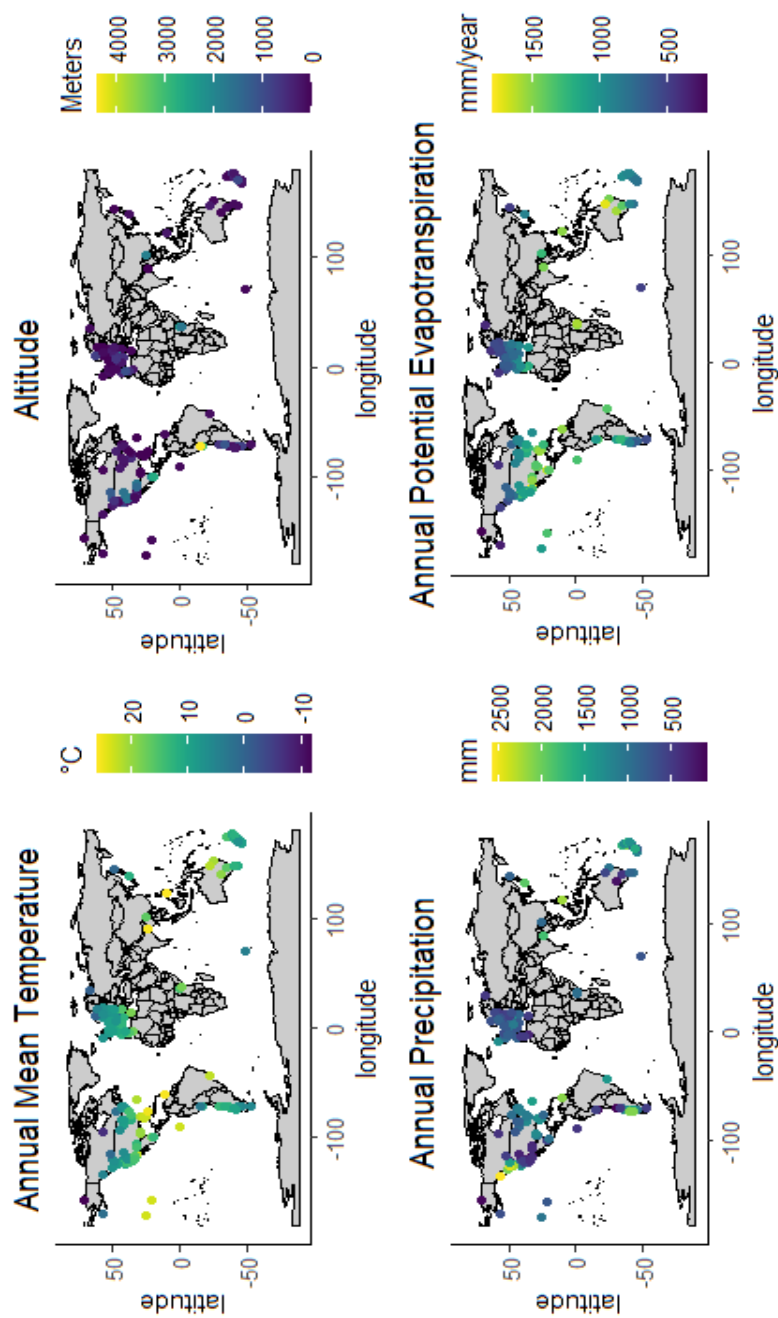


Figure 1. The average environmental variable data from each sample location. Each point represents one or more of the sample locations from the edited PROCEED version 5.0 database. A 50 square kilometer buffer was used to represent the average conditions of the environment around the sampled point.

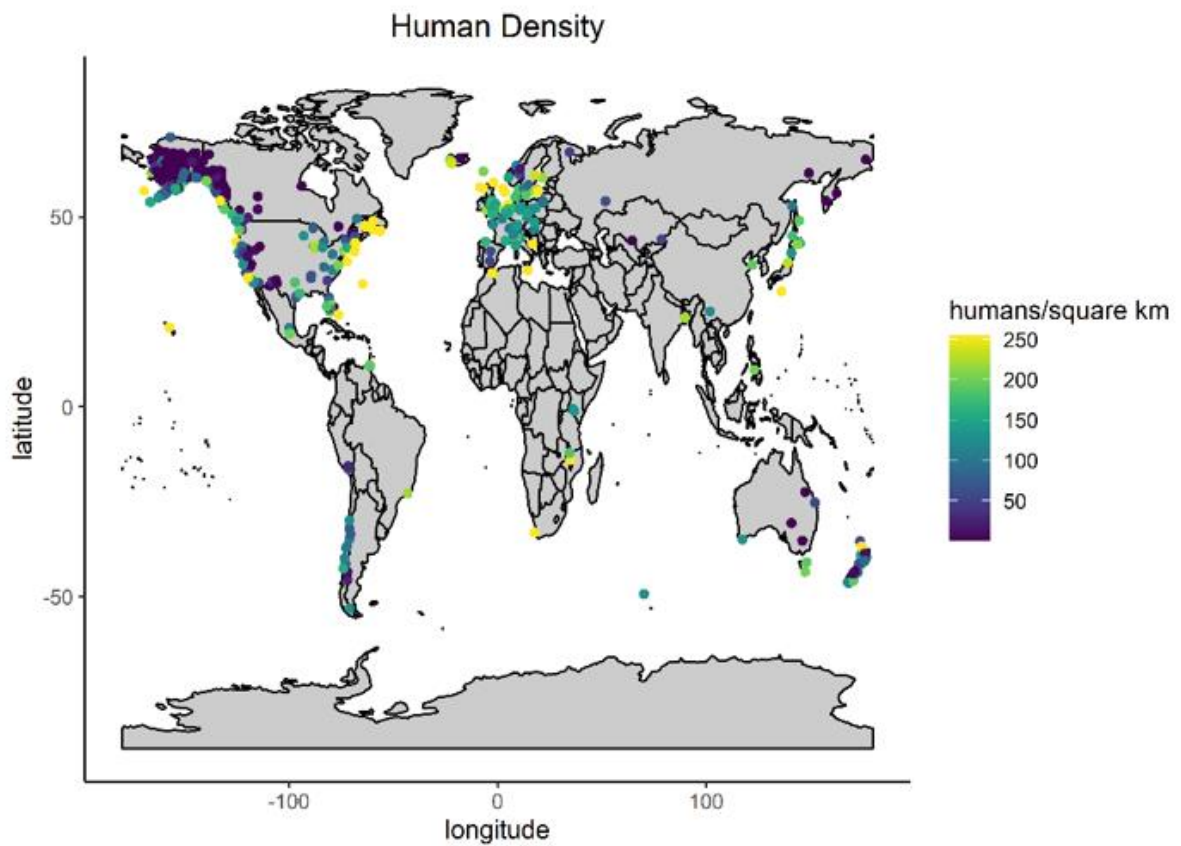


Figure 2. The average human density from each sample location (50 km^2). Each point represents one or more samples from the locations of the edited PROCEED version 5.0 database samples. A 50 square kilometer buffer was used to represent the average conditions of the environment around the sampled point.

Data Spatial Patterns

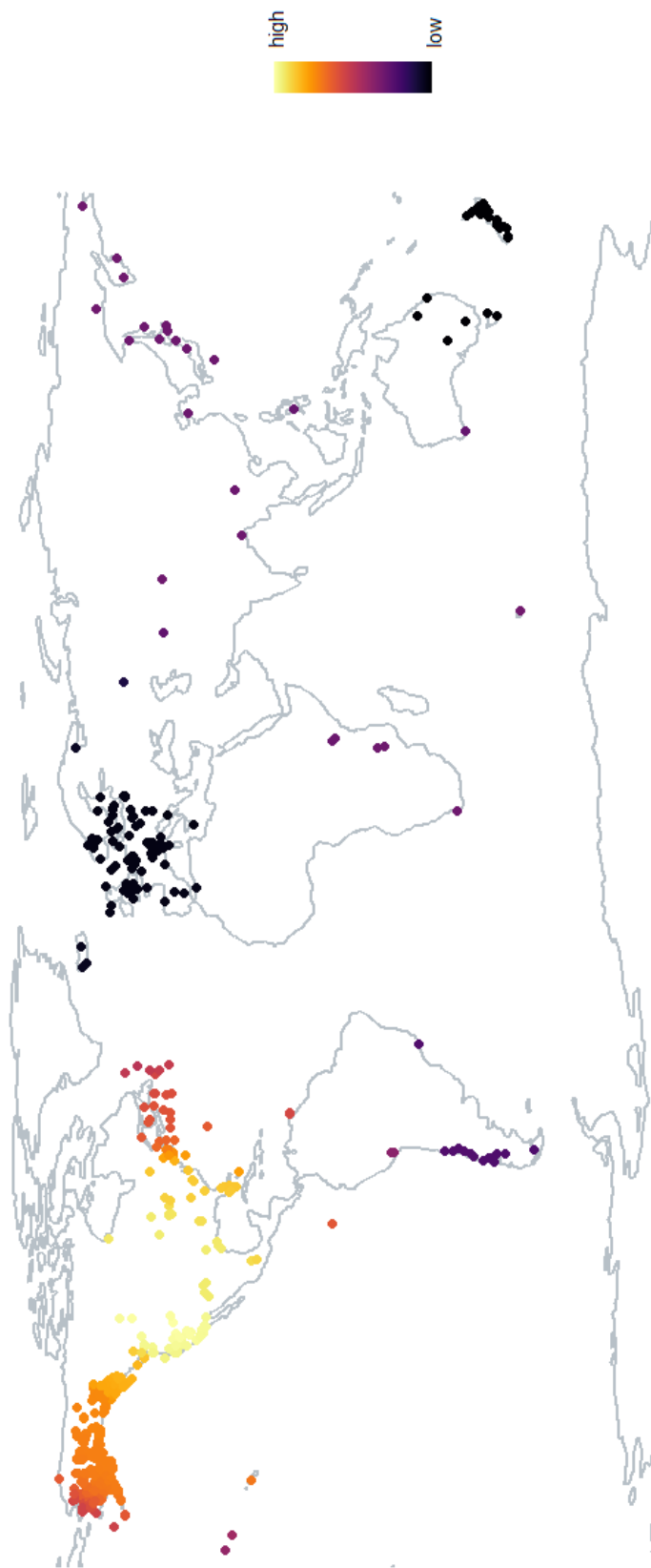


Figure 3. The relationship between the adaptive rates and spatial scale patterning. Each point represents one or more samples with varying degrees of spatial scale patterning in the edited PROCEED version 5.0 database. Adaptive rates were calculated in Haldanes and Darwins based on statistical differences.

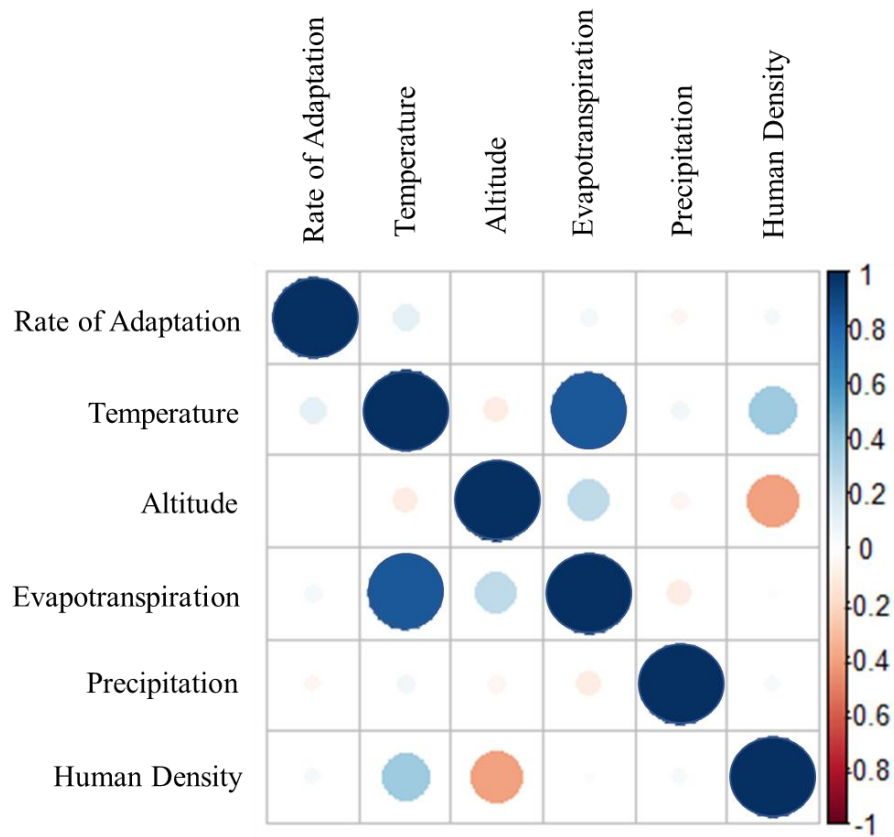


Figure 4. Data correlation matrix for each analyzed variable. The correlation coefficients for each averaged environmental variable and the rate of adaptation in units of Darwins and Haldanes.

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Appendix

Table A1. List of included species. The list of names and frequency of each species included in the edited PROCEED version 5.0 dataset.

Species Name	Frequency
<i>Abrothrix longipilis apta</i>	14
<i>Abrothrix olivaceus brachiotis</i>	28
<i>Abrothrix sanborni</i>	14
<i>Acrocephalus scirpaceus</i>	2
<i>Aedes albopictus</i>	324
<i>Aegithalos caudatus</i>	1
<i>Agrostis capillaris</i>	1
<i>Agrostis stolonifera</i>	1
<i>Akodon xanthorhinus xanthorhinus</i>	14
<i>Alauda arvensis</i>	1
<i>Alliaria petiolata</i>	63
<i>Alopex lagopus</i>	2
<i>Anolis sagrei</i>	44
<i>Anser caerulescens caerulescens</i>	5
<i>Anthoxanthum odoratum</i>	4
<i>Anthoxanthum odoratum L.</i>	6
<i>Anthus campestris</i>	1
<i>Anthus pratensis</i>	1
<i>Anthus trivialis</i>	1
<i>Aphelocoma ultramarina</i>	1
<i>Apus apus</i>	1
<i>Apus melba</i>	1
<i>Betula pubescens</i>	4
<i>Branta leucopsis</i>	8
<i>Brassica rapa L.</i>	6
<i>Bufo marinus</i>	3
<i>Calliphora vicina</i>	4
<i>Carduelis cannabina</i>	1
<i>Carduelis carduelis</i>	1
<i>Carduelis chloris</i>	1
<i>Carduelis spinus</i>	1
<i>Carduus nutans</i>	3
<i>Cervus elaphus</i>	2

<i>Cervus elaphus hispanicus</i>	1
<i>Cervus elaphus scoticus</i>	3
<i>Chaetodipus fallax fallax</i>	14
<i>Chionomys nivalis</i>	6
<i>Clidemia hirta</i>	33
<i>Coccothraustes coccothraustes</i>	1
<i>Coturnix coturnix</i>	1
<i>Cygnus olor</i>	5
<i>Cytisus scoparius</i>	4
<i>Delichon urbica</i>	1
<i>Deschampsia cespitosa</i>	4
<i>Digitalis purpurea</i>	3
<i>Dipodomys merriami merriami</i>	14
<i>Drosophila subobscura</i>	540
<i>Echium vulgare</i>	3
<i>Elymus multisetus</i>	48
<i>Emberiza cia</i>	1
<i>Emberiza hortulana</i>	1
<i>Emberiza schoeniclus</i>	1
<i>Erithacus rubecula</i>	1
<i>Festuca ovina</i>	4
<i>Ficedula albicollis</i>	2
<i>Ficedula hypoleuca</i>	3
<i>Fringilla coelebs</i>	337
<i>Fringilla montifringilla</i>	1
<i>Garrulus glandarius</i>	1
<i>Geospiza fortis</i>	12
<i>Geospiza scandens</i>	9
<i>Herpestes javanicus</i>	20
<i>Hippolais icterina</i>	1
<i>Hirundo rustica</i>	3
<i>Hydromantes strinatii</i>	1
<i>Hypericum perforatum</i>	2
<i>Hypochaeris radicata</i>	2
<i>Jadera haematoloma</i>	102
<i>Junco hyemalis</i>	2
<i>Jynx torquilla</i>	1
<i>Lactuca muralis</i>	2
<i>Lanius collurio</i>	2

<i>Larus audouinii</i>	12
<i>Lemmus trimucronatus nigripes</i>	14
<i>Locustella fluviatilis</i>	5
<i>Locustella naevia</i>	1
<i>Lophuromys flavopunctatus zena</i>	15
<i>Loxia curvirostra</i>	2
<i>Lullula arborea</i>	1
<i>Luscinia megarhynchos</i>	1
<i>Lythrum salicaria</i>	28
<i>Macropus giganteus</i>	5
<i>Macropus rufogriseus</i>	5
<i>Malaclemys terrapin</i>	21
<i>Martes foina</i>	2
<i>Melaleuca quinquenervia</i>	60
<i>Microtus mexicanus mexicanus</i>	14
<i>Microtus pennsylvanicus pennsylvanicus</i>	28
<i>Motacilla alba</i>	1
<i>Motacilla cinerea</i>	1
<i>Motacilla flava</i>	1
<i>Mus musculus</i>	3
<i>Muscicapa striata</i>	1
<i>Mustela erminea</i>	16
<i>Mustela frenata</i>	4
<i>Oenanthe oenanthe</i>	1
<i>Oligoryzomys longicaudatus philippii</i>	14
<i>Onthophagus taurus</i>	29
<i>Oryctolagus cuniculus</i>	57
<i>Ovis aries</i>	12
<i>Ovis canadensis</i>	15
<i>Pararge aegeria</i>	4
<i>Parus ater</i>	1
<i>Parus caeruleus</i>	10
<i>Parus major</i>	8
<i>Passer domesticus</i>	395
<i>Passer montanus</i>	1
<i>Passerella iliaca</i>	147
<i>Peromyscus leucopus</i>	15
<i>Peromyscus leucopus noveboracensis</i>	14
<i>Peromyscus maniculatus anacapae</i>	16

<i>Peromyscus maniculatus blandus</i>	14
<i>Peromyscus maniculatus elusus</i>	16
<i>Peromyscus maniculatus nubiterrae</i>	14
<i>Peromyscus maniculatus santacruzae</i>	16
<i>Phoenicurus ochruros</i>	1
<i>Phoenicurus phoenicurus</i>	1
<i>Phylloscopus collybita</i>	1
<i>Phylloscopus sibilatrix</i>	1
<i>Phylloscopus trochilus</i>	1
<i>Phyllotis xanthopygus chilensis</i>	30
<i>Pieris rapae</i>	12
<i>Pitangus sulphuratus</i>	6
<i>Plantago major L.</i>	33
<i>Podarcis sicula</i>	30
<i>Praomys jacksoni</i>	15
<i>Prunella modularis</i>	1
<i>Pseudechis porphyriacus</i>	1
<i>Pyrrhula pyrrhula</i>	1
<i>Rana arvalis</i>	12
<i>Rana esculenta complex</i>	6
<i>Rangifer t. tarandus</i>	8
<i>Rattus tanezumi mindanensis</i>	15
<i>Regulus ignicapillus</i>	1
<i>Regulus regulus</i>	1
<i>Riparia riparia</i>	1
<i>Saussurea laniceps</i>	2
<i>Saussurea medusa</i>	1
<i>Saxicola rubetra</i>	1
<i>Scathophaga stercoraria</i>	2
<i>Sciurus carolinensis pennsylvanicus</i>	14
<i>Senecio jacobaea</i>	3
<i>Senecio squalidus</i>	18
<i>Senecio sylvaticus</i>	2
<i>Serinus citrinella</i>	1
<i>Serinus serinus</i>	1
<i>Silene latifolia</i>	18
<i>Sitta europaea</i>	1
<i>Solidago canadensis</i>	6
<i>Solidago gigantea</i>	32

<i>Spartina alterniflora</i>	4
<i>Sterna paradisaea</i>	1
<i>Sturnia philippensis</i>	2
<i>Sturnus vulgaris</i>	1
<i>Sylvia atricapilla</i>	1
<i>Sylvia borin</i>	1
<i>Sylvia communis</i>	1
<i>Tachyoryctes splendens naivashae</i>	10
<i>Tamias striatus griseus</i>	15
<i>Telespyza cantans</i>	20
<i>Thomomys umbrinus umbrinus</i>	13
<i>Tristerix corymbosus</i>	6
<i>Troglodytes troglodytes</i>	1
<i>Turdus iliacus</i>	1
<i>Turdus merula</i>	1
<i>Turdus philomelos</i>	1
<i>Turdus torquatus alpestris</i>	1
<i>Turdus torquatus torquatus</i>	1
<i>Turdus viscivorus</i>	1
<i>Ulex europaeus</i>	4
<i>Urocyon littoralis</i>	1
<i>Ursus arctos</i>	13
<i>Zosterops lateralis</i>	40
<hr/> Total	<hr/> 3216