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Potential for Speciation in Mammals Following Vast, Late Miocene Volcanic
Interruptions in the Pacific Northwest

by

Ryan Thomas Paul McKenna

A thesis submitted in partial fulfillment of the
requirements for the degree of

Master of Science
in
Geology

Thesis Committee:
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Abstract

The impact of large-scale volcanic eruptions on landscapes can affect many processes ranging from interrupting or redirecting regional soil forming processes and hydrological systems to generating temporary changes in global climate. Though more studies exist every year, less is known of the direct impact of large-scale volcanic eruptions on ecosystems and extinction, while even less is known of their impact on speciation. In deposits throughout the Pacific Northwest a special combination and association of volcanic magnitude with palaeoecological yield frequently presents unique prospects for inquiry. In this study, particular attention is given to large, late Miocene ash-flow tuffs of central and eastern Oregon, the Rattlesnake Tuff among them. Additionally, a scenario is tested whereby populations become isolated from one another across the expanse of ash-flow tuff and enclosed by nearby physical barriers. Exploration into this scenario and the effects of ecological recovery on speciation in mammals are made through a cellular automaton created here and speciation modeling by H.A. Orr. The cellular automaton is validated by a small data set from New Zealand with results of all models compared to studies in ecology, the fossil record, genetics, and island evolution. Results suggest ecosystem recovery is much faster than mammalian species origination rates. Though evolution in mammals is known to occur over relatively short intervals of time (10^1 - 10^3 yrs), based on model comparisons, primary productivity generally returns to its carrying capacity two orders of magnitude (10^2 - 10^3 vs. $\geq 10^4$ yrs) faster than mammalian speciation.

For Rebecca,
there's no place else like us.

Acknowledgements

I first considered the effects of large ash-flows on ecological recovery and mammalian diversity during a paleontology internship at John Day Fossil Beds NM in the summer of 2005. In the beginning it seemed ash-flows were common to every time period represented by the outcrops we prospected. Later on, working out the stratigraphy with the help of then staff paleontologists Ted Fremd, Scott Foss, Regan Dunn, and Matt Smith, I realized I was observing a few, very extensive ash-flows. I specifically recall being tested by Scott Foss as he pointed to the Rattlesnake Tuff, which at the time seemed like a random tuff in the hills overlooking his house in Dayville, Oregon. That same tuff was literally—nearly at eye level—eroding into Regan Dunn’s backyard further east in Mt. Vernon. To later find out the Rattlesnake Tuff is also in outcrops more than 150 km south was nothing less than mind blowing. This undetermined relationship between extensive ash-flows and ecological and evolutionary responses was branded into my thoughts when I internshipped again at the Monument in 2007 following the completion of my Bachelor’s degree in Geology at PSU. Without these people and my experiences working at the Monument this study likely never happens.

Nearing the end of my second internship at the Monument, I was approached by Mike Cummings, advisor to my Honor’s thesis and undergraduate degree, to see if I would like to continue my education and assist in teaching in the University Studies and Geology Departments at Portland State University. When I pitched my research idea to Mike I had little notion as to what numerical or field methodologies I would, should, or could use to conduct or focus the research. Mike never batted an eye. He is an advisor

whose guidance has always served me well. In my experience, Mike, as an advisor, is an inquirer, not a supervisor. In my opinion, this characteristic engenders genuine discussion and necessary intellectual growth. Since, at times, the process of conducting research can have precarious effects on human emotions; this approach has served to bring balance to these moments of uncertainty. Mike has always made me feel we are on equal ground. I cannot say enough how this has helped me. Thanks fall short.

Others who directly helped me with this thesis also served as counselors in building it a more solid foundation. The other members of my committee (Christina hulbe and Jeff Fletcher) stand out the most. Christina gave many weeks to the thesis overall, but she most especially helped me with taking thoughts and concepts of the ecological problem into the model I built. Like Christina, Jeff helped me with the modeling, but he also asked questions I would never have thought of that no one else did either. Additionally, I thank Martin Streck for data he provided, general discussions on large-scale ash-flow tuffs, and his honesty and support.

This thesis fulfills the requirements for my second degree from PSU's Geology Department. Much talk is made in the student lounge speculating on the best way to continue one's education; to stay or move on. As I have gradually met different people with different backgrounds from different departments in different schools I conclude the world is what you make of it. I believe this thesis honors this sentiment and the hours, weeks, months, and years I, and all those involved in the Geology Department, have devoted to an undeniably greater end.

With that, I thank the Geology Department for the education and empowerment it has provided me. I now have access to internal resources that allow me to pursue my own

ideas to completion. This is highly gratifying. I also thank my graduate and undergraduate comrades for their patience, companionship, many conversations, and undeserved help and beer over the years we have shared common spaces and goals. I would also like to thank Barb Shaw and Tom Lindsey. Barb, Tom and I for quite a while were likely the only three people on campus with a pure, unadulterated interest in paleontology. For all the wonders of hydrogeology, landslides, or just plain basalt that are present in the department, it's been nice to know I'm not alone. There is a knowing familiarity I feel we have that we share with no one else. Perhaps Cameron Tompkins can take my place if he hasn't already.

Beyond the department and campus, I would like to acknowledge the patience and love of all my friends. Many of my friends in Portland have never known me to *not* be in school. I am also forever severely indebted to the love, patience, and support of my family. We are apart for such long periods I feel like Rip Van Winkle when I see them.

Lastly, my wife Rebecca is responsible for giving me the confidence to go to school in the first place, so I blame her the most. Thus, after nearly four years of operating in good faith with as much due diligence while mustering up the courage of my convictions, my chance to shine has been in rolling with the punches and going with the flow...

Parkview
Portland, Oregon
April 15, 2010

R.T.P. McK

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Acronyms

AE	-	Actual Evapotranspiration
AGCM/ML	-	Atmospheric General Circulation Model/Mixed Layer model
AWL	-	Abundant, Widespread, and Long-lived
BDMI	-	Bateson-Dobzhansky-Muller Incompatibilities
CLAMP	-	Climate-leaf Analysis Multivariate Program
CPER	-	Central Plains Experimental Range
DvCT	-	Devine Canyon Tuff
ERM	-	Ecosystem Recovery Model
FVC	-	Fractional Vegetation Cover
GEM	-	General Ecological Model
LMPN	-	Late Miocene Pacific Northwest
MAP	-	Mean Annual Precipitation
MAT	-	Mean Annual Temperature
MRT	-	Model Recovery Time
NAAP	-	Net Annual Aboveground Primary Productivity
NAFMSD	-	North American Fossil Systematics Database
ORT	-	Observed Recovery Time
PCT	-	Prater Creek Tuff
PNW	-	Pacific Northwest
RST	-	Rattlesnake Tuff
SLOH	-	Sleep-or-Hide

Chapter 1

Introduction

“The slow changes of a million years of evolutionary time must yield to the rapidly fluctuating requirements of ecological time.”

-Stephen J. Gould, 1977

Large-scale ash-flow eruptions deposit massive quantities ($10^{13} - 10^{15}$ kg) of volcanic ash, pumice, and lithics across extensive areas (10^4 km²) over short periods of time ($10^3 - 10^5$ s; Bursik and Woods, 1996). These flows rapidly and severely disrupt everything they contact on the ground surface. The disruption of geological surficial processes (Manville, 2000), geomorphological features (e.g. in-filled valleys), and climate (Rampino and Self, 1992, 1993; Jones et al., 2007; Cathers et al., 2010) demonstrate this power. As for scale, the Rattlesnake Tuff (RST; Streck and Grunder, 1995)—a high temperature ($\sim 860^\circ\text{C}$ pre-eruptive temperature; Streck and Grunder, 2008) ash-flow tuff in central Oregon— was most likely deposited 1) in no more than a day and 2) over more than 40,000 km². In comparison, the ecological unit for the migrating herds of the Serengeti—a roughly flat, west-sloping plateau—is approximately 25,500 km² (Schaller, 1972; Figure 1). Given this potential for widespread disruption, how might members of surrounding ecological communities respond: evolve with the opportunity of new found isolation or subsequent equitable acreage, or simply resume their roles after the interruption?

Figure 1. Comparison between areal extents of the RST in central Oregon (brown) and Serengeti National Park in Tanzania (blue). The yellow circular area is a hypothetical total area covered by the RST eruption. The white dot represents the proposed source of the RST.

1.1 Specification of methodologies

Ecological modeling is performed in this study to assist in the investigation of potential speciation in mammals following vast, late Miocene volcanic interruptions in the Pacific Northwest. This is done because the resolution of both the local and global fossil records are “generally too coarse in temporal scale and too limited in geographic coverage to provide a detailed history of speciation events (Erwin and Anstey, 1995).” No data on repeated fossil mammal originations in the Pacific Northwest exist immediately following large ash-flows like the RST because of scarcity of fossils in collections or a lack of stratigraphic and temporal control in these terrestrial systems.

Moreover, adequate details to distinguish speciation or ecosystem recovery times in these stratigraphic sections are not available.

Unfortunately, one relatively simple preexisting model that uses general theory and observations around primary succession phenomena (e.g., root competition, albedo effects of volcanic ash surfaces on climate) with the goal of understanding the timing of ecosystem recovery is not available, and so had to be created. With a deficiency in data from the stratigraphic and fossil record of the late Miocene Pacific Northwest (LMPN), models that require specific parameters, variables, or interactions (e.g. nitrogen concentrations, species composition, forest population dynamics, transition probabilities, groundwater hydrogeology, etc.) that cannot be accounted for in order to produce the appropriate output are not used. Models such as the resource-ratio hypothesis (Tilman, 1985), JABORA/FORET forest simulation model (Huston and Smith, 1987), Markov models (Gibson et al., 1997, Childress et al., 1998), and general ecological models (Fitz et al., 1996) fall into this category. Thus, for example, with no known estimates for nitrogen levels in ancient soils and ash-flow surfaces of the LMPN, models that require nitrogen input were not used.

The model generated for this thesis is a cellular automaton (CA). This discrete model uses stochastic, non-agent, rule-based algorithms with different “states” (e.g. “on” vs. “off”) and allometric relationships for generating output regarding ecosystem recovery times of net annual aboveground primary productivity (g m^{-2}) and large mammalian herbivore biomass (g m^{-2}). Recovery time results of this ecosystem model are compared to timing in speciation probability from models developed by Orr (1995) and

Orr and Turelli (2001) of allopatric speciation from complex hybrid incompatibilities.

These models are described in Sections 3.3.1 and 3.5, respectively.

Chapter 2

Patterns, processes, and hypotheses

The following chapter describes the patterns and processes involved in understanding the background to the ash-flow-speciation relationship investigated in this study. It is subdivided into sections regarding biotic patterns (i.e. diversity in the fossil record, preservation of organic materials, and body mass distributions) and abiotic patterns (i.e. depositional extents of ash-flows, paleotopography, and climate), as well as biotic processes (i.e. isolation of populations and interactions in species population parameters: abundance, distribution, and lifespan). Much of the work has been summarized from the literature with the exception of new syntheses I have generated to further enrich the reader's understanding of the patterns and processes (i.e. Figure 2, Figures 4A-C, and multimodality tests in Section 2.1.3). Additionally, a premise and hypotheses are formulated.

Primary interest in this report concerns whether or not radial sheet pyroclastic flows act as an adequate barrier to gene flow within and among species populations to impose the evolution and establishment of Mayr's peripheral (1963) or secondary (2001) isolates (observed, in this case, as new species suddenly appearing in the fossil record). Neodarwinian genetics suggests species evolve as microevolutionary processes produce gradual changes predominantly through natural selection on mutation and adaptation (Coyne and Orr, 2004) while macroevolutionary patterns in the fossil record most frequently document rapid appearances in species followed by long periods of evolutionary stasis—a pattern best known as punctuated equilibrium (Eldredge and Gould, 1972; Gould and Eldredge, 1993; Gould, 2002). Moreover, Gutschick and

BassiriRad (2003, 2010) consider extreme events, like disturbance, an integral and common ingredient for evolution while Grime (1973), Horn (1975), and Connell (1978) suggest intermediate levels of disturbance maintain the highest species diversity.

In the fossil record of the Pacific Northwest (PNW), it is difficult to discern an eruption-speciation relationship from fossil remains alone. Firstly, some strata record changing and oscillating environments and faunas interbedded with volcanic deposits (Retallack et al., 2004). Secondly, many volcanic eruptions, in part, are responsible for the preservation of the underlying basins where fossil remains are found and consequently, disrupt any apparent pattern. For example, the Rattlesnake local fauna of the late Miocene fanglomerates and paleosols west of Dayville, Oregon documents one such instance where only fragments of the mammalian assemblage (as well as similar paleosol characteristics) resume locally above the previously mentioned RST (Merriam et al., 1925; Retallack et al., 2002; T. Fremd, pers. comm., 2007). Generally, where the RST is found it is the uppermost horizon. Furthermore, highly fossiliferous terrestrially-born sediments are generally few and far between.

2.1 The biotic patterns

The pattern of mammalian diversity in the PNW fossil record through the last 45 million years (Figure 2) is generated from database faunal lists in the Paleobiology Database's North American Fossil Mammal Systematics Database (NAFMSD). Fossil mammal, time-range data were collected from the NAFMSD that originally came from localities within a 400-km radius centered on the proposed source area of the RST near Capehart Lake, Oregon (Streck and Grunder, 1995; Figure 3). Figure 2 illustrates non-

volant, non-aquatic, terrestrial, fossil eutherian (placental) mammals of the PNW through time (see Appendix A for details on the collection of the data and creation of Figure 2). Twelve relatively large volcanic eruptions (vertical dashed lines) overlay the taxon ranges (horizontal solid lines). Care must be taken in the interpretation of data in Figure 2. First, taxon temporal ranges are likely to be less than their true duration (Foote and Raup, 1996). Second, temporal ranges of the taxa are based solely on occurrences within temporally determined geologic formations.

Figure 2. Temporal ranges of eutherian mammals in the Cenozoic Pacific Northwest (horizontal lines). Vertical lines indicate specific volcanic eruptions. The grey block is the period of eruption of the Columbia River Basalt Group (Camp and Ross, 2004). I) A/B Tuff (30 Ma); II) Picture Gorge Ignimbrite (28.7 Ma); III) Deep Creek Tuff (27.5 Ma); IV) Biotite Tuff (27.2 Ma); V) Tin Roof Tuff (25.3 Ma); VI) ATR Tuff (22.6 Ma); VII) Grand Ronde Basalt (16 Ma); VIII) Mascall Tuff (15.8 Ma); IX) Devine Canyon Tuff (9.68 Ma); X) Prater Creek Tuff (8.48 Ma); XI) Rattlesnake Tuff (7.05 Ma); XII) Huckleberry Ridge Tuff (2 Ma).

Figure 3. Shaded relief image of the PNW. The area of fossil mammal collection is indicated by the white circle ($\sim 500,000 \text{ km}^2$) and description in Section 2.1.

2.1.1 Abundant, widespread, and long-lived species

Abundant, widespread, and long-lived (AWL) species are most frequently preserved in the fossil record (Bennett, 1990; Foote and Raup, 1996; Barnosky, 2001; Vrba and DeGusta, 2004). From a statistical standpoint, this is known as length-biased sampling (Solow and Smith, 1997). AWL species tend to be overrepresented in the fossil record while rare species are likely never preserved. Spatial and temporal considerations

regarding preservation probability and genetic drift also indirectly assume newly evolved species begin as relatively small peripherally or secondarily isolated local “founder” populations. There are tests in the fossil record to support this (Vrba and DeGusta, 2004; Millien, 2006) and tests in genetic laboratories to oppose it (Rundle et al., 1998; Rundle, 2003).

2.1.2 Preservation of new species

Preservation of newly evolved mammal species will likely be from the bones of large mammals. Preferential preservation of large mammals over small mammals is favored by two main modes of destruction. Behrensmeyer et al. (1979) argue that a greater degree of trampling, predation, and scavenging destroy small bones more frequently due to lower tissue density of small skeletal elements. Retallack (1988), however, argues for a stronger chemical durability of large bones due to their lower surface area to volume ratios against the effects of acidic dissolution. Both modes of destruction are likely occurring to some extent simultaneously at any given time. A discussion on preservation modes is synthesized in Lyman (1994; but also see Behrensmeyer et al., 2000).

2.1.3 Modality in eutherian body mass distributions

Considering preservation biases in favor of large mammals, body size frequency distributions appear to indicate a roughly inverse relationship to diversity (Figure 4A). This would suggest that new species produced by large eruptions are small-sized mammals in small, isolated populations, and thus, less likely to be preserved compared to

large mammals. Figure 4A illustrates a unimodal body mass distribution in non-volant, non-aquatic, terrestrial eutherian mammals of late Quaternary North America (~50,000 years to Present). Brown and Nicoletto (1991) explain this unimodal pattern to be the result of higher speciation rates and diversity at approximately 100 g (4 to 5 ln g units). When they compared eutherian species across space in present-day North American biomes (i.e. grasslands, taiga, eastern forest), the result is species in the 100 g size range differ across space within the same biomes, while the smallest and largest species tend to be alike. This unimodal trend has been shown to exist on other continents (e.g. Africa and South America; see Lyons et al., 2004) as well as in biogeographic zones (e.g. the Nearctic and Afrotropics; see Lovegrove and Haines, 2004). Modern 100 g-sized mammals have relatively low preservation probabilities and are not widespread, while concurrently most diverse. These general and relatively uniform results have led to the suggestion of an optimal body size of ~100 g in terrestrial mammals (Brown et al., 1993; Brown, 1995; Chown and Gaston, 1997; Johst and Brandl, 1997; Alroy, 1998, 2003; Marquet and Taper, 1998; Gardezi and de Silva, 1999; Lovegrove and Haines, 2004). One hundred grams is also close to the average size of Cretaceous mammals (Alroy, 1998).

Figure 4a-c. Frequency distributions relative to body mass of a) late Quaternary North American mammals, b) Cenozoic North American mammals, and c) Cenozoic North American Pacific Northwest mammals. Modality in the late Quaternary distribution is unimodal while the distributions for Cenozoic North America and Cenozoic Pacific Northwest are bimodal. Data for the late Quaternary is from Smith et al. (2003). Data for the Cenozoic North America is adapted from Alroy (1998). Data for Cenozoic Pacific Northwest is gathered in this study and described in Appendix C. Explanations and discussion of these distribution patterns can be found in the text.

The paleontological record suggests a more bimodal pattern in body mass distributions (Alroy et al., 1998, 2003) than the late Quaternary record. This is demonstrated in the fossil record of valid North American fossil mammals in Figure 4B

(duration of time unknown, but as a possible minimum representing the entire Cenozoic Era—the past 65 Ma). Several explanations have been put forward regarding the pattern. The first explanation is a pattern itself known as Cope’s Rule, wherein taxa—and more specifically, lineages—increase non-randomly in size over time. E.D. Cope (1887) was the first to suggest this pattern after analyzing North American Paleocene faunas. Much later, the first in-depth quantitative study confirmed the pattern for fossil mammals of North America (Alroy, 1998). No underlying cause for the pattern described by Cope’s Rule was given in this report, except for the suggestion that a second unstable optimal size limit exists in mammals which perhaps has yet to become predictable. Three more explanations are introduced below. Potential explanations for the second emergent, but unstable mode are 1) low speciation rates, high extinction rates, or both (Alroy, 1998); 2) locomotory adaptations for speed (i.e. digitigrade and unguligrade from plantigrade) inadvertently increased the size of terrestrially-bound mammals (Lovegrove and Haines, 2003; however, initial tests of this explanation have not been universally positive); 3) large mammals are vulnerable to extinction via intense environmental changes while smaller mammals typically exhibit hibernation, torpor, or burrowing behaviors which act as an environmental buffer termed “sleep-or-hide” (SLOH) behavior (Liow et al., 2008).

The dual-optima of eutherian body mass modes are clear in the Cenozoic PNW (Figure 4C). Probability of multimodality for this data set is 0.95 indicating strong bimodality (Silverman, 1981; Jones, 1983; see Appendix B for details into test methodology). The result is congruent with Lovegrove and Haines’ (2003) suggestion

that subregional scales provide surplus structural detail in body mass distributions over scales larger than zoogeographical scales (i.e. continents).

2.2 The abiotic patterns

The abiotic patterns in the LMPN are divided into descriptions of three large-scale ash-flow tuffs, its paleotopography, and its climate. These three sections illustrate the general environmental background of the LMPN and the logic for assumptions made in the modeling to come.

2.2.1 Three large-scale LMPN ash-flow tuffs

Three spatially extensive ash-flow tuffs stand out in the landscape and stratigraphy of central Oregon: the Devine Canyon Tuff, Prater Creek Tuff, and previously mentioned Rattlesnake Tuff (Figure 5). Table 1 lists important features of the three tuffs. All three tuffs have devitrified and welded portions indicating very high temperatures upon eruption (Greene, 1973; Walker, 1979; Streck and Grunder, 1995). Maximum thicknesses range up to and greater than 30 meters. Rocks in outcrop above and below each of these tuffs include lacustrine, fluvial, alluvial, and volcanic deposits, though the RST tends to have sparsely preserved overlying rocks with one particular exception being the John Day Valley. Formations comprising and adjacent to these tuffs are in Table A.2 in Appendix A.

Table 1. Some important features of three large-scale ash-flow tuffs in central Oregon erupted over a period in the LMPN from 10-7 Ma.

Tuff	Age	Original Area	Source	Age Reference
Rattlesnake Tuff (RST)	7.05 +/- 0.01 Ma	50,000 km ² ; Walker, 1979	Capehart Lake, western Harney Basin	Streck and Grunder, 1995
Prater Creek Tuff (PCT)	8.48 +/- 0.05 Ma	not estimated	undetermined	Dieno and Grunder, unpub.
Devine Canyon Tuff (DvCT)	9.68 +/- 0.03 Ma	> 18,600 km ² ; Streck and Ferns, 2004	Harney Basin	Dieno and Grunder, unpub.

2.2.2 Terrain and relief in the LMPN

The RST is relatively uniform in thickness typically 15-30 m thick with greatest and least thicknesses at approximately 70 and 5 m, respectively. Interpretation inferred from this range in thickness is that of a low relief landscape at the time of the eruption. This is supported by a large number of nearly complete sections (recording multiple welding facies) throughout most of the outcrop area. According to Streck and Grunder (1995), a “more rugged topography would have generated thicker valley deposits thinning outward with a more patchy distribution pattern,” while Streck and Grunder (2007) note that the RST is “among the farthest traveled pyroclastic flows currently known.” Ash fall from the Rattlesnake Tuff eruption very likely was deposited as far south as northern Nevada in the Thousand Creek Formation. According to Perkins et al. (1998), ash collected in the Thousand Creek Formation “is an excellent match to basal fallout tuff we collected from the 7.05 Ma Rattlesnake Tuff...in the Harney Basin, Oregon.” Unlike the RST, less about the thickness uniformity of the PCT and DvCT is known regarding the topographic relief present at the time of deposition. However,

thicknesses between 10 and 20 m are found in 54% of Greene's (1973) measured DvCT sections ($n = 28$). The DvCT's area is perhaps comparable to the Taupo Ignimbrite on the North Island of New Zealand (area = 20,000 km²). Figure 5 illustrates the areas of general outcrop extent from mapping for the three tuffs.

Figure 5. Areal extent of Devine Canyon Tuff (DvCT), Prater Creek Tuff (PCT), and Rattlesnake Tuff (RST; 30,000–40,000 km²) amidst regions of high elevation throughout the time spanning the eruptions (10–7 Ma). Images A and B hail from central and eastern Oregon, respectively. Image A is from the Devine Canyon on Highway 395. Upper tuff is the RST and the lower tuff is the PCT. Image B is an image of the DvCT near Juntura viewed from the road to Chucker Campground. Modified from Streck and Ferns (2004).

Topographic barriers noted by Streck and Grunder (1995) are the Strawberry and Aldrich Mountains. However, multiple topographic features potentially acting as migration barriers may have been present between 10–7 Ma (Figure 5). Appendix C describes much of the elevation, fluvial, and basinal features understood to be present in the LMPN.

2.2.3 LMPN climate

Atmospheric circulation patterns constructed using an atmospheric general circulation model and a mixed layer ocean model (AGCM/ML) for the late Miocene indicate western North America experienced similar climate conditions and changes with the seasons to today (Steppuhn et al., 2006). Steppuhn et al. (2006) report the atmospheric circulation over the Pacific Ocean to be in a permanent El Niño state. Model reconstructions of the paleoclimate are supported by terrestrial proxy data (Micheels et al., 2007; Steppuhn et al., 2007).

Local estimates of mean annual precipitation (*MAP*; mm/yr) and mean annual temperature (*MAT*; °C) in the LMPN may be made using fossil leaves and paleosols. Using his climate-leaf analysis multivariate program (CLAMP), Wolfe (1994) established estimates for *MAT* from fossil leaves in the middle Ellensburg Formation (~10 Ma) in south central Washington as 12.3°C and in the late Miocene Troutdale Formation of Oregon west of the Cascades as 11.7°C. Applying Wolfe's CLAMP, Buechler et al. (2007) give a *MAT* of 13.4°C from the late Miocene (10.5-8.5 Ma) Pickett Creek Flora in Owyhee County, Idaho. Buechler et al. (2007) also give a precipitation estimate of 690 mm for an approximately eight month growing season.

Retallack (2007) has conducted extensive studies generating estimates for *MAP* and *MAT* from paleosols spanning much of the Oligocene to Holocene of central and eastern Oregon including 104 measured and analyzed paleosols that comprise the late Miocene sub-epoch (11.608 - 5.332 Ma; Tortonian and Messinian Stages). *MAP* estimates from Bk horizon depths (corrected for compaction) in paleosols give an average

range of 235 - 517 mm/yr from 46 sampled horizons (~10-7 Ma). Chemical analyses of $\text{Al}_2\text{O}_3/(\text{Al}_2\text{O}_3+\text{CaO}+\text{Na}_2\text{O})$ molar ratios yield *MAP* estimates for six late Miocene paleosols (~7 Ma) range on average from 521 - 885 mm/yr. Retallack (2007; North American paleosol database by Retallack) estimates MAT from chemical analyses of $(\text{Na}_2+\text{K}_2\text{O})/\text{Al}_2\text{O}_3$ molar ratios of the same six paleosols is 11.3°C with an average range of 6.9 - 15.7°C. Table 2 summarizes the *MAP* and MAT values for the LMPN.

Table 2. LMPN climate data from fossil leaves and paleosols. MAT column illustrates the range first and then the average. Note the difference in *MAP* values for Retallack's (2007) chemical composition and Bk horizon depth methods. The Bk horizon depth estimations are for paleosols in an adequately dry environment to form Bk (aka calcic) horizons, whereas the chemical composition estimations are made from clay deposits in wetter environments that have higher weathering rates and thus reflect higher *MAP* values. Additionally, the number of samples for Bk horizons is much greater than for molar ratios. NAPD is short for North American paleosol database.

Location	Formation/ Flora	Age	MAT	MAP	Method	Reference
central Oregon	Rattlesnake Fm.	7.2 - 7 Ma	6.9 - 15.7°C; 11.3°C	521 - 885 mm/yr	chemical composition	Retallack (2007; NAPD)
central Oregon	multiple fms.	10 - 7 Ma	na	235 - 517 mm/yr	Bk horizon depth	Retallack (2007; NAPD)
south- central Washington	middle Ellensburg Fm.	~ 10 Ma	4.6 - 20.0°C; 12.3°C	na	CLAMP	Wolfe (1994)
Oregon, west of Cascades	Troutdale Fm.	~ 10 Ma ?	3.8 - 19.6°C; 11.7°C	na	CLAMP	Wolfe (1994)
Owyhee Co., Idaho	Pickett Creek Flora	10.5 - 8.5 Ma	2.8 - 24.0°C; 13.4°C	690 mm/8 mo. growing season	CLAMP	Buechler et al. (2007)

2.3 General premise and hypotheses

With the general LMPN biotic and abiotic patterns in mind, a general premise and hypotheses are presented below. An additional section describes circumstances regarding isolation in local populations. These sections attempt to incorporate and synthesize the general biotic and abiotic patterns and processes into a testable approach for explaining the potential for speciation.

2.3.1 Premise

Three propositions and a conclusion are as follows:

- Punctuated equilibria are predominantly observed in fossil taxa (Gould, 2002; Geary, 2009).
- Allopatric (dichopatric and peripatric)¹ speciation is the classic mode of speciation proposed as a mechanism for the many rapid originations observed in the fossil record (Eldredge and Gould, 1972).
- Taggart and Cross (1990) describe ecological recovery and volcanic interruptions of ecosystems as "disturbance or destruction by local volcanic activity...followed by distinct seral stages, barring further disturbance, leading to the *reestablishment* [my emphasis] of a diverse...community mosaic."

¹ Dichopatric speciation (aka, vicariant allopatric speciation) is the origination of new species in isolation where a physical barrier crosses a once continuous geographic range of a species population (e.g. flooding of the Bering Strait at the end of the Pleistocene Epoch isolating Alaska and Siberia; Mayr, 2001). Peripatric speciation is the origination of new species in isolation due to dispersal of a subset of a species population to areas beyond the periphery of the species range (e.g. species dispersal to islands from mainland populations; Mayr, 2001).

- Geologically instantaneous large-scale pyroclastic eruptions coupled with nearby increases in elevation or uncrossable water bodies provide adequate isolation to generate new dichopatric species before ecosystems return to their former states reuniting populations.

2.3.2 Hypotheses

To evaluate the premise outlined above, two hypotheses are formed; a null (H_0) and an alternate (H_1). The hypothesis to be tested is

$$H_0: t_R \cong \min(t_S)$$

which states that recovery time (t_R) following large-scale eruptions is approximately equal to the minimum time for speciation (t_S) in eutherian mammals. This is tested against the alternate

$$H_1: t_R < \min(t_S)$$

which states that t_R following large-scale eruptions is less than $\min(t_S)$ in eutherian mammals (Figure 6).

Figure 6. Conceptual illustration of the relationship between recovery time t_R and speciation time t_S for the A) null hypothesis H_0 and B) the alternate H_1 . In (B) H_0 is rejected.

At the center of these hypotheses is the interplay between evolutionary time and ecological time. Will the relatively rapid changes and processes in ecological time intersect the slower evolutionary time scale provided by the potential evolutionary circumstances of large-scale ash-flows? Or, does t_R encourage Futuyma (1987) and Eldredge's (2003) ephemeral "sloshing bucket" of gene pools over time? The consequences for these hypotheses are that no potential for speciation lies in the premise

if a t_R approximately equal to the $\min(t_S)$ is not met. Without having met this criterion it is unlikely large-scale pyroclastic eruptions coupled with migration barriers like nearby increases in elevation will generate new mammal species.

2.3.3 Isolation of populations and communities

Isolation is intended in this section to describe only the physical, geographic isolation of populations and communities; not the "isolating mechanisms" of the Modern Synthesis (Dobzhansky, 1937; Huxley, 1942; Mayr, 1942; Simpson, 1944; White, 1945; Rensch, 1947; Stebbins, 1950) and all the genetic bases for pre- and postzygotic barriers intrinsic to sexual reproduction explored thereafter. Much of what was written in Section 2.1.1 on AWL species aligns well with what follows regarding population size and distribution.

Of the four main evolutionary processes (mutation, migration, natural selection, and random genetic drift), migration is most closely related to geographic isolation. Once isolated, a population or community will no longer have access to the allelic variability of the parent population or community. A disconnected population thus is composed of vicariant populations and may potentially generate reproductively isolated allopatric species if enough time has passed for adequate genetic differentiation to arise and persist (Mayr, 1954, 1982, 2001). If a population is severely cut-off from the parent population with only a sampling of the parent population's variability, large genetic changes may occur relatively rapidly forming a dichopatric (Mayr, 2001) or peripatric (Mayr, 1982, 2001) species from the peripheral isolate. The dichopatric mode coupled with physical barriers and a large eruption is illustrated in Figure 7.

Figure 7. Illustration of the potential effects of a large-scale ash-flow eruption coupled with nearby physical barriers like increases in elevation. Vicariant populations recover from their respective isolation. Given the populations are strongly isolated, the duration of time spent recovering the former species distribution is unknown. The fragmented populations are dichopatric.

One example of isolation due to physical barriers concerns small mammals at high elevations in the Great Basin. In a now well-known study, Brown (1971) found that species of small mammals living in the "montane islands" of the Great Basin were isolated from each other by a "sea of sagebrush desert." These species migrated in the wetter glacial periods of the Pleistocene and became isolated during interglacials. On the largest "islands" the diversity of small mammals is unchanged from the "mainland" populations east and west of the Great Basin while the smaller "islands" have experienced extinction.

Schaller (1967) observed that habitat requirements restricted the movements of ungulates in India. In particular, barasingha (*Cervus duvauceli*), along with other ungulates in India, tend to avoid steep terrain. At the time of Schaller's study he noted that "another factor which has influenced the distribution of the barasingha is their avoidance of extensive steep terrain like the foothills of the Himalayas. The large grass meadows of Corbett Park have been in existence at least since 1840, but they have not been colonized, the animals having failed to venture over the one or two ridges that separate their habitat in the plains from that in the foothill valleys (1967)."

Whether surrounded by water or different environments, islands are the best examples of how changes in species arise due to isolation from parent populations; studies on the diversity of finches on the Galapagos Islands are certainly the most popularized example of peripheral isolates. Island isolation is not as "messy" as mainland isolation because constraints on temporal development and spatially distinguishable boundaries are more readily observed. Studies of biological evolution on islands exist for both modern (Lomolino, 1985, 2005; Schmidt and Jensen, 2003; Bromham and Cardillo,

2007; Meiri et al., 2008; Losos and Ricklefs, 2009) and ancient (Lister, 1989; Millien, 2006; Raia and Meiri, 2006) settings. Generally, morphological changes are studied most (e.g. body size in the "island rule"). This appears to be valid since morphological changes are generally observed most frequently over behavior, physiology, and life history traits (Mousseau and Roff, 1987). In this study however, the key to understanding the potential duration of isolation in the "mainland" setting of the LMPN will depend on the length of time for recovery following such large ash-flows like the RST, PCT, and DvCT. This is made more apparent since examples of adequate detail on morphological change above and below these tuffs is not known.

Chapter 3 Methods

3.1 General overview of methods

Three possible approaches to address the previously described ash-flow-dichopatric speciation scenario in Sections 2.3.1-2.3.3 (Figure 6) are: 1) perform extensive field work to obtain collections of data from multiple deposits in outcrops above and below major ash-flows to determine any pedological, floral, and faunal changes; 2) complete rigorous analytical and statistical methods on fossil data from multiple well-defined stratigraphic sections with deposits above and below major ash-flows to determine any significant trends; 3) model a process or processes associated with the scenario and apply the model to particular identified or inferred conditions. Only the third option was investigated here. It is described below taking the form of a cellular automaton (CA).

3.2 Method and model selection

A cellular automaton representing ancient ecosystems is considered here an appropriate model design for establishing recovery times in the LMPN. There is limited knowledge on specific details typically included in studies of modern systems for which to apply to paleoecosystem dynamics in this study of the LMPN. Moreover, accounting for a plethora of processes involved in ecosystem interactions, responses, and patterns known in modern settings is difficult to manage in a model with regard to the relative paucity of paleoenvironmental and paleoecological data. Additionally, data with regard to the LMPN is typically coarse in spatial and temporal resolution, and therefore, such

averaging automatically contains reductions in small-scale process variability.

Inclusion of numerous processes with unknown boundaries ought to be limited in modeling short space and time scales in studies of past geologic periods. Nevertheless, there are some processes that could not be avoided including spatial and temporal inhibition and disturbance and seedling establishment rates.

Many model types exist to represent ecosystems. Such ecological model types can be viewed as roughly falling into five categories: unstructured, biologically-structured, individual-based, metapopulation, and landscape (spatially explicit) models. The following paragraphs attempt to briefly explain what these model types are and reasons for their rejection. The first three model types are generally not given spatial structure (Munns et al., 2007).

Unstructured models in ecology are generally deterministic models that describe populations in terms of abundance and density. For example, coupled Lotka-Volterra predator-prey ordinary differential equations predict predator-prey population cycles. However, beyond the laboratory these cycles are rarely observed in nature (DeRoos and Persson, 2005). Thus, they are generally deemed empirically unsuccessful by ecosystem modelers (Odenbaugh, 2005).

Biologically-structured models represent systems with ages, stages or classes. Stages can be demographic, developmental, size, or genetic. They are generally density-independent and deterministic (Munns et al., 2007). It is possible to apply biologically-structured models to primary succession scenarios based on intermediate stages in succession. However, this type of modeling requires data on plant abundance and

diversity. Data of this kind are not available from the stratigraphic and fossil records of the LMPN.

Individual-based (aka agent-based or entity-based) models focus on single entities rather than groups of entities. Gap models are likely one of the most used examples of this type. With respect to primary succession, Huston and Smith (1987) applied the JABOWA/FORET forest simulation gap model to pairs of species with contrasting characteristics (e.g., shade tolerance vs. intolerance). Individual-based models like the JABOWA/FORET gap model usually require specific data on species and their characteristics. A similar model is the grassland gap model (STEPPE) of the Central Plains Experimental Range in north-central Colorado (Coffin and Laurantroth, 1990). Despite the near congruency of biomes between characteristics of the modern grassland steppe of north-central Colorado and the shrub steppe of the LMPN (e.g., mean annual precipitation ranges and vegetation types), deficiency in species-specific data regarding the shrub steppe of the LMPN stands in the way of successfully executing the STEPPE gap model. Additionally, no stipulation is made to whether the model is for primary or secondary succession. Since its initial conditions have organic soil present—and, at times, additional fertilizer from cow dung “disturbance”—secondary succession is the likely succession type modeled. Thus, the STEPPE gap model also requires modification for application in a primary succession scenario.

Metapopulation models consider population dynamics between disjunct populations across space. These disjunct populations are segregated subunits connected by migration and can be used at both individual-based or population levels (Munns et al., 2007). There likely are some metapopulation dynamics at work in a recovering

ecosystem $\geq 10^3 \text{ km}^2$ as would have existed following the ash-flow eruptions of the LMPN. However, fully developing a model on such a scale with computer software is perhaps unrealistic at this time. Ideally, for example, a primary succession model would simulate process interactions of all known species and their characteristics at the individual (m^2 ?) scale over $\geq 10^{10}$ (m^2 ?) cells through $\geq 10^2$ iterations (e.g. days, months, years) allowing individuals to establish randomly, grow, mature, reproduce, aggregate into patches, and begin the process of colonization through facilitation, competition and secondary succession barring any subsequent, but more frequent and less severe, disturbances (e.g., fire or flood). Here, the dynamics may even be illuminated more or less continuously to understand how observed seral stages can develop. This type of model would have a high degree of realism.

Certain assumptions allow this effort to be avoided for models built to retrieve ecosystem recovery times (Section 3.3 outlines these assumptions and more in greater detail.). First, establishment of seedlings in space is random (Walker and del Moral, 2003). Second, for what little data exist on recovering ecosystems following ash-flow eruptions, distance from the eruptive source and thickness of deposits are not significant factors to the rate of recovery (Whilmshurst and McGlone, 1996). Third, local climate is correlated with recovery rates (Whilmshurst and McGlone, 1996). Fourth and finally, it is assumed here, any single patch that recovers 90% of its biomass carrying capacity is a proxy for full recovery of the entire initially disturbed surface; that is, given a patch is at 90% of its biomass carrying capacity, it is unlikely that an adjacent patch is at 0-5% of its biomass capacity.

Landscape (a.k.a. spatially explicit) models, unlike metapopulation models, model organism movement and interactions continuously across space. They represent specific landscapes, specific organism movements and interactions, and species-specific properties (Munns et al., 2007). Such specificity promotes accuracy and realism over generality. The exception to this would be the general ecosystem model (GEM) by Fitz et al. (1996) intended “for use across a wide range of ecosystem types.” Methods used in landscape models employ GIS software (e.g., Topping, 1999) or rule-based cellular automata (CA; e.g., Fuentes and Kuperrman, 1999). Because CA-based landscape models track organism movement and interactions across any adjacent cells in a matrix, CA-based landscape models can be considered a special case of metapopulation models. The argument used above for rejecting the use of metapopulation models for modeling data-deficient paleoecosystem recovery also applies to landscape models regarding heterogeneous landscapes. Furthermore, the GEM is not used because the hydraulic properties of the recovering groundwater systems are unknown for the LMPN.

3.2.1 Model generality

Odenbaugh (2005) defines the relative contrast between general and specific models as: “A model is more general than another model [if] the former successfully represents a larger number of systems than the latter.” The model that follows does this in that it uses overall biomass per area rather than any specific attribute of individuals of a species. Much of the modeling developed for the above described methods have highly specific characteristics built for specific ecological problems in the modern world. Assessing risks to or managing ecosystems promotes the need for a high degree of

specificity and realism in many research endeavors. Furthermore, these different methods are supported by richness in data paleoecological settings do not possess. More often than the applied cases, pure research has tended to approach primary succession from the perspective of understanding its generalities. However, the consensus is that “no general theory of succession has emerged that can predict the dynamics of species replacements in many different habitats (Walker and del Moral, 2003).” Few specific plant species are known in the LMPN fossil record. For the purposes of modeling vegetation dynamics in LMPN paleoecosystems, ecosystem biomass recovery is used instead of species succession.

3.3 Model assumptions

The following assumptions provide a conceptual framework for a recovering ecosystem from the initial state of sterilization to the carrying capacity of the system. The assumptions are:

- 1) Death and eradication of life on the landscape (i.e. sterilization) is complete following deposition of ash-flow tuffs. Large magnitude ($10^3 - 10^4 \text{ km}^2$) tuffs of the LMPN are too hot and too thick for buried plants to emerge from burial (del Moral and Grishin, 1999) and plants are most likely incinerated.
- 2) Ash flow surface temperatures are not likely to interfere with ecological recovery for any extended period of time since surface cooling to below 100°C has been measured to be within 100 days (Kozu, 1934; Riehle, 1973).
- 3) Local climate is associated with recovery rates (Wilmshurst and McGlone, 1996; Walker and del Moral, 2003). Furthermore, albedo of the ash surface is likely

important to local climate due to the altering of surface temperatures and their interaction with overlying air masses (Cross and Taggart, 1982; Jones et al., 2007).

- 4) Seedling establishment is random (Walker and del Moral, 2003). Additionally, area and distance from the margin are not significant to recovery rates.

Wilmshurst and McGlone (1996) observed from pollen analyses variable recovery times across the 20,000 km² Taupo ash-flow that were unrelated to distances to the source of the eruption. Regarding estimated recovery times, the site nearest to the source (Ongarue) recovered the fastest. This is likely due to wind dispersal. For example, del Moral (1998) reports that on very isolated pumice at Mount St. Helens, 50% of the plants present are wind dispersers.

- 5) Temporal changes in biomass are closely associated with species change (Walker and del Moral, 2003).
- 6) The ecological landscape is recovered once 90% of the biomass carrying capacity has been reached (Coffin and Laurenroth, 1990). It is unlikely a patch has 0-5% of its biomass capacity if an adjacent patch is at 90% capacity. Moreover, similar root trace fossils, mean annual precipitation (mm yr⁻¹) estimates, and textures in paleosols above and below the Rattlesnake Tuff (Retallack et al., 2002) provide evidence that LMPN paleoecosystems recover to their former states following large-scale eruptions. Modern studies on eruptions such as Taupo, New Zealand (Wilmshurst and McGlone, 1996), Mt. St. Helens, USA (Wood and del Moral, 1987), El Chichòn, Mexico (Burnham, 1994), and Montagne Pelée, Martinique (Beard, 1976) make similar observations as well.

3.4 An ecosystem recovery model

An ecosystem recovery model (ERM; Figure 7 & Appendix D) was made to establish recovery times for plant primary productivity following large ash-flow eruptions in the LMPN. The following describes parameters and formulas of the ERM (see also Table 3).

Table 3. Model parameters, descriptions, and dimensions for the steps in the model that follow. In the last column for disturbance d and seedling establishment rates E values in parentheses are for the LMPN while values not in parentheses are for recovery on the Taupo Ignimbrite. nd indicates dimensionless values. See text for details regarding parameter values.

Parameter	Description	Dimensions	Value
a	albedo	nd	0 - 1
MAP	mean annual precipitation	mm yr ⁻¹	Varying
AE	actual evapotranspiration	mm yr ⁻¹	Varying
$NAAP$	net annual aboveground primary productivity	g m ⁻²	Varying
FVC	fractional vegetation cover	nd	0 - 1
d	disturbance rate	yr ⁻¹	0.042 (0.13) - 0.01 (0.037)
E	seedling establishment rate	yr ⁻¹	0.05 (0.05) - 0.3 (0.3, 0.2, 0.15, 0.1)

The model domain is a one dimensional ring of square meter plots. Variables in each plot are albedo (a ; 0-1), mean annual precipitation (MAP ; mm yr⁻¹), actual

evapotranspiration (AE ; mm yr^{-1}), net annual aboveground primary productivity ($NAAP$; g m^{-2}), and fractional vegetation cover (FVC ; 0-1). One feedback is built into the model with a directly dependent on FVC after the first year. Initial albedo values, a_0 are randomly sampled from a uniform distribution with a range of 0.38 to 0.7 as measured from wet and dry ash of the Bishop Tuff in Jones et al. (2007; approximated from Figure 2).

From a_0 , linear and nonlinear regressions estimate all variables except FVC , which is estimated from the ratio of plots with biomass to total number of plots (see formulas in Table 4). The significance of the fit of the linear equations assumes normality of the residuals and is estimated from p values, while residual graph analyses are applied to estimate the goodness of fit of the nonlinear equations.

Table 4. Formulas used to estimate the different variables. Residual graph analyses were performed on the nonlinear relationships. All data are global in scale with the exception of the $MAP - a$ relationship formed only from North American data subsets of global data sets. See text for details.

Relationship	Formula	Data Source
$MAP - a$	$MAP^{-1} = 0.0136 \pm 0.0012(a)^{1.5436 \pm 0.1048}$	Huffman et al., 1997 (MAP); Barkstrom et al., 1990 (a)
$AE - MAP$	$AE = 0.6719 \pm 0.0171(MAP)^*$	multiple; see Appendix E
$NAAP - AE$	$NAAP = 0.1854 \pm 0.2477(AE)^{1.3318 \pm 0.1968}$	Rosenzweig, 1967
$a - FVC$	$a = -0.8569 \pm 0.8272(FVC)^2 + 0.4744 \pm 0.9377(FVC) + 0.4605 \pm 0.2270$	multiple; see Appendix D

* $p < 0.05$

Recovery is repressed by disturbance and seedling establishment mortality. Two sets of frequencies are used. The pioneer stage of recovery representing the first 30 years

in the model has different disturbance d and seedling establishment E rates than a post-pioneer stage (see Table 3). The greater values of d are the pioneer stage disturbances and the smaller values are for time thereafter. Smaller values for E are the pioneer stage seedling establishments and the greater values are for time thereafter.

Disturbances in ecosystems in recovery on ash surfaces have high rates initially with respect to pre-eruption d due to increased aridity caused by properties of the ash surface and lightening caused by friction of ash particles in the atmosphere (Cross and Taggart, 1982; Wilmshurst and McGlone, 1996; Walker and del Moral, 2003; Jones et al., 2007). d —number of disturbances per time period—is generally discussed in terms of return intervals until the next disturbance, or presented as a percentage of areal extent disturbed. For the first 30 years of the post-eruption Taupo surface d is set at 0.042 (estimated from number of charcoal samples per recovery time in Wilmshurst and McGlone, 1996). For levels of a pre-eruption d simulation studies give a guideline. They have applied a range of “low” to “high” d . For instance, Plotnick and Gardner (2002) use a range of d from 0 to 0.4 in their landscape ecology model. Turner and Dale (1991) applied frequencies of 0.01, 0.1, and 0.5 to represent low, moderate, and high levels of disturbance in their landscape disturbance model. Botta and Foley (2002) applied d equal to 0.005, 0.01, and 0.02 to a simulation study of Amazonian ecosystem dynamics. None of these reports validated their reasoning for using such ranges or values. Nevertheless, d is tuned here within these ranges for recovery on the Taupo surface to meet recovery times estimated by Wilmshurst and McGlone (1996; see Table 3 above). The tuned d is 0.01 (one disturbance in 100 years). For the LMPN, pioneer post-eruption d are set at 0.13 from the highest mean fire disturbance return interval for the shrub steppe ecosystem

near Paisley, Oregon reported in Miller and Rose (1999). The lowest fire disturbance return interval of 0.037 from Miller and Rose (1999) is used for post-pioneer stage d .

The value of a disturbance is thus a randomly sampled value up to the limit of the per plot carrying capacity $NAAP_{\max}$ at rate d . If a disturbance at year j is greater than plot i , plot i equals zero. Otherwise, biomass value disturbed is subtracted by the biomass in plot i .

Few studies make an explicit connection between field observations and seedling establishment rates appropriate for ecosystem models. Pioneer stage seedling establishment rates (denoted hereafter as E) for both Taupo and LMPN post-eruption surfaces are set at 0.05 from estimates of establishment of *Epilobium* *gustifolium* and *Anaphalism* *argaritace* on the Pumice Plains of Mount St. Helens by Wood and Morris (1990) in the early stages of its recovery. Since seed and seedling desiccation is the greatest cause of mortality in establishment (Fenner and Thompson, 2005) a low E would likely persist for some time in the pioneer stage. Takenaka (2006) used values of E ranging from 0.001 to 0.3 in a simulation study of seedling population dynamics. This range was applied in the ERM. Taupo pre-eruption E were tuned to 0.3. LMPN pre-eruption E were difficult to determine. They were likely to be less than that of Taupo with regard to increased seed desiccation, and thus, seed mortality, in the more arid climates of the LMPN. For completeness in the ERM, E equal to 0.3, 0.2, 0.15, and 0.1 were used. E less than 0.1 tended to rarely recover fully.

Glenn-Lewin and van der Maarel (1992) define inhibition as “the prevention of plant maturation or growth, or, especially, the prevention of plant establishment, by existing plants.” Spatial inhibition is produced from biomass differences with plot i

compared to plots $i-1$ and $i+1$. If both $i-1 > i$ and $i+1 > i$, i dies. Temporal inhibition is produced from root biomass differences with plot i compared to incoming seeds at time $j+1$ to $j+m$ which may establish themselves in plot i . In a root competition experiment, Gersani et al. (2001) concluded overlapping plant root systems compensate for sharing a common space with limiting below ground resources (water, nutrients, and soil/substrate porosity; Walker and del Moral, 2003) through 85% increased root growth. Plants of the same species were potted simultaneously. Here, if a resident plot's root biomass is 85% greater than an incoming root system it has a 15% advance on the root growth increases both root systems will undertake. This allows the resident root system to dominate acquisition of limiting below ground resources. If resident root biomass is less than 85% of incoming root biomass the resident cannot dominate resource acquisition and is unable to compete with an incoming plant with greater resource acquisition efficiency; the resident will be, in effect, "crowded out" of its plot. This is a bias in the succession of smaller, short-lived plants toward larger, longer-lived plants. However, if the resident root biomass is neither less than 85% of the incoming root biomass nor greater than total incoming root biomass, both root systems become established in the plot. This action is meant to simulate the potential for the formation of thickets of the same species which may later inhibit other species (Walker and del Moral, 2003). Additionally, if the incoming root biomass is simply less than the resident root biomass, the resident lives on while the invasive never establishes itself in the plot. Forest root:shoot biomass ratios are multiplied by $NAAP$. As $NAAP$ increases in forests recovering on the Taupo Ignimbrite surface root:shoot ratios go from 0.456 at $NAAP < 750 \text{ g m}^{-2}$ to 0.226 at $750 \text{ g m}^{-2} <$

$NAAP \leq 1500 \text{ g m}^{-2}$ to 0.241 at $NAAP > 1500 \text{ g m}^{-2}$. Root:shoot biomass ratios for the LMPN are set at 1.837 for shrublands. Root:shoot ratio data from Mokany et al. (2006).

Each year begins with an estimate of *MAP* from albedo followed by *AE* from *MAP* estimations, and then *NAAP* from *AE* estimations (Figure 8). Seedlings are established and disturbed. Established seeds that survive compete with any adjacent plots and any incoming plants. *FVC* of the plots is estimated and used to generate albedo values for the next year. The ecosystem is considered recover the first year 90% of the biomass carrying capacity is reached.

Figure 8. General diagram of model flow of steps described in Section 3.3.1. Steps within the loop are repeated across all plots and all years.

3.5 Model limitations

Limited data are available with which to constrain the present model (Table 5). The strength of work is in the empirical relationships and in the application of lessons from experiments and syntheses of data in the literature on competition and post-eruption aridity. Unfortunately, there is considerable uncertainty regarding general estimates of E and d despite the attention they receive in the literature (Walker, 1999; Walker and del Moral, 2003). Additionally, little is known about the effect of vast eruptions on groundwater.

Table 5. Degrees of uncertainty in the ERM. Considerations of different factors important to ecological recovery are not all present in the model. In general, empirical relationships and data from experiments are more applicable to paleoecosystem recovery in this effort than microsite surface properties or groundwater hydrology development due to data availability.

Less	<-----	----->	More
AE - MAP relationship	MAP - a relationship	E	Surface crusts
$NAAP$ - AE relationship	a - FVC relationship	d	Groundwater hydrology
	Post-eruption aridity	root competition	
		light competition	

3.6 Model validation

To validate the ERM, the goal to generate model recovery times (MRT) similar to observed recovery times (ORT) following the Taupo eruption on the North Island of New Zealand in 1850 BP (Table 4). The methods used are an Anderson-Darling test for normality, single sample sign test of the medians, and the Brown-Forsythe test of equal

variances. The steps involved are 1) to run 100 consecutive model runs; 2) test for normality using an Anderson-Darling test and the freeware software CumFreq (waterlog.info/cumfreq); 3) testing for a significant difference in the medians with a single sample sign test of the medians, and variances with Brown-Forsythe's test of equal variances.

Table 6. Observed recovery times for five sites on the North Island of New Zealand that followed the Taupo eruption in 1850 BP (Wilmhurst and McGlone, 1996). Mean annual precipitation ranges come from the National Institute of Water and Atmospheric Research (www.niwa.co.nz).

Site	Recovery Time (yrs)	MAP (mm yr ⁻¹)
Ongarue	120	2000 - 1500
Lake Rotonuiaha*	145	2000 - 1500
Lake Tutira**	175	1500 - 1250
Tunapahore	200	1250 - 1000
Kohika	225	1250 - 1000

* Wilmhurst and McGlone (1996) report a MAP of 2000 mm/yr

** Wilmhurst and McGlone (1996) report a MAP of 1400 mm/yr

It is unknown if the ORT's are at or near the mean or if they fall elsewhere in a potential normal or lognormal distribution since no standard deviation or error was given by Wilmhurst and McGlone (1996) regarding their estimates shown in Table 6 above. Existing model output is a result of the inputs and the calibration to allometric relationships as well as the design of the model components and assumptions.

3.7 Cumulative probability and waiting time models for allopatric speciation.

Orr (1995) focused on modeling speciation as a process of accumulating genic incompatibilities in allopatrically diverging populations. These incompatibilities, known as Bateson-Dobzhansky-Muller incompatibilities (BDMI's), are a conceptual model first described by Bateson (1909) and later discussed independently by Dobzhansky (1936) and Muller (1939, 1940). In this model (Figure 9) two separated populations with identical genotypes inherit different mutations to identical genes that later become fixed (i.e. genes with no other form (allele) in the population to substitute). When the populations encounter each other at a later time, after a physical barrier to migration no longer exists or is overcome, their hybrids are either inviable or sterile. It is also possible for just one population to undergo genetic change forming incompatible hybridizations with populations possessing ancestral genotypes (Muller, 1942).

Figure 9. BDMI cartoon of a barrier-induced reproductive incompatibility. See text for details.

Orr (1995) modeled three scenarios: a single incompatibility, multiple incompatibilities, and complex incompatibilities among protein-coding genes. Orr (1995) suggests complex incompatibilities are more common than the first two for two main reasons: 1) complex incompatibilities substitute more nucleotides (i.e. three is more than two, four is more than three) per mutation, thus accruing more changes to the population; 2) single incompatibilities are often prevented by the generation of an unfit genotype (e.g. genotype AA is compatible with aa , but neither are compatible with Aa where A is the

dominant allele and a is recessive). The model for complex incompatibilities is as follows:

$$S \approx 1 - \exp\left(-\sum_{n=2}^K p_n \binom{K}{n}\right). \quad (1)$$

Here S is the cumulative probability of speciation, K is the number of base pair substitutions, n is the number of loci involved in an incompatibility, p_n is the probability of each of the n incompatibilities and $\binom{K}{n}$ is the binomial coefficient indicating the number of combinations of K substitutions taken n loci at a time and formulated as $\binom{K}{n} = K!/(n![K-n]!)$.

Values to the variables in Equation 1 were chosen using Orr's (1995) report as a guide. K increases from 0 to ∞ and n is set at 7 loci—the maximum number at which the fraction of possible paths from ancestor to successor stabilizes. Setting an upper limit with $n = 7$ for complex incompatibilities should assist in generating the “fastest” possible speciation rate from Equation 1 because it is likely any speciation related to eruptions like the RST, PCT, and DvCT occurs along shared time intervals between ecosystems and evolution. Values for p_n are more difficult to apply because there are few data on the probability of incompatibilities. Orr and Turelli (2001) estimated $p_n = 10^{-6}$ or less. Their estimations were made from the fruit fly *Drosophila* and the fire-bellied toad *Bombina*. For these estimates, they did not model for complex incompatibilities, going only as far as multiple incompatibilities. Therefore, higher probabilities than what they suggest to be reasonable, however wild in their application, are explored to increase the rate at which speciation occurs in mammals. p_n values ranging from 10^{-6} to as high as 10^{-4} are applied here following Orr (1995) and Gavrillets (2004).

To obtain an estimated waiting time to allopatric speciation t_s (years) a formula developed by Orr and Turelli (2001) and discussed in Gavrillets (2004) is used. The formula is

$$t_s = \frac{Q}{2w}. \quad (2)$$

Q is the number of substitutions required for reproductive isolation and w is the substitution rate. The coefficient of 2 represents a parent and daughter population pairing.

Q is estimated from Equation 1 when $S \approx 1$. Relating speciation to eutherian mammals, substitution rates are estimated for house mice (*Mus musculus*; 2.2×10^{-9} substitutions/site/year; Waterson et al., 2002) and humans (*Homo sapiens*; 4.5×10^{-9} substitutions/site/year; Waterson et al., 2002) by multiplying the per site substitution rates by the number of protein-coding genes (house mice and humans have been estimated at 20,210 and 19,042 protein-coding genes, respectively; Church et al., 2009). The bimodal pattern of the number of taxa with increasing mass (Figure 4A-C) has two modes in the region of 50-150g and 60-160kg. House mouse and human masses each lie near or in the two respective modes as illustrated in Figure 4C and described in Section 2.1.3. Since their masses are in the modes of greatest diversity this suggests speciation may be highest at these two modes.

Additionally, to explore the difference in evolutionary rates as observed by Millien (2006) of mammalian fossil island taxa compared to their mainland counter parts, t_s is divided by 3.1. This step is intended to simulate a more rapid (punctuated) change in a LMPN eutherian mammal population.

One advantage of Orr's (1995) and Orr and Turelli's (2001) models (Equations 1 and 2) is that unlike others (c.f., Gavrillets, 1999; Lynch and Force, 2000; Kondrashov,

2003) they require no population estimates. Population variables generally accompany the genetic variables in these modeling efforts. Though density estimates are possible for members of paleobiological communities using allometric equations, these models are simple and general enough to provide a rough estimate, and that is all that is required for this study. The importance of these speciation models is to have a quantitative representation of the process of speciation for comparison to the process-based ERM described above. The intention is meant to support further qualitative and semi-quantitative estimates of the time for speciation obtained from studies of the patterns of speciation. Two disadvantages of Equations 1 and 2 are that they strictly represent the genetic inheritance system and biological species concept.

Chapter 4

Results

4.1 Validation

ERM median and variance output run for the Taupo scenario comparing model recovery times (MRT) and observed recovery times (ORT) indicate there is no statistical difference (Table 7). Additionally, 100 runs of MRT output are not normally distributed. Log-normal distributions are found in many reports other recovery times (Lawrence, 1988). Though the processes for time to recovery from illness in *Homo sapiens* and ecosystem recovery on barren landscapes are different, they illustrate similar event-time data types. Furthermore, the ERM is designed similarly to Kapteyn's Analogue Machine for positively skewed distributions (Aitchison and Brown, 1957). In this machine, nine rows of $\triangle$ -shaped wedges divide sand in two directions, left or right. In the ERM (Figure 7), the state-based steps are analogous to the wedges.

Table 7. Validation results for the model recovery times (MRT's) and observed recovery times (ORT's) following the Taupo eruption. The MRT data are not normally distributed, while the median and variance cannot be determined to be significantly different from the median and variance of the ORT data.

Parameter	MRT (yrs)	ORT (yrs)	Single Sample Sign test	Brown-Forsythe test	Anderson-Darling test
Median	183.5	175	Test statistic= 0.99 $t_{crit, \alpha=0.05} = -1.64$		
Standard Deviation	72.67	41.92	W = 0.491 $F_{crit, \alpha=0.05, 1, 103} = 3.9$		
<i>n</i>	100	5	$A^{*2} = 15.18$ $A^2_{crit, \alpha=0.05} = 0.751$		

4.2 Model stability

Stability of the model is assessed using standard deviations (Figure 10). The standard deviation decreases as time increases unless further disturbance occurs removing or reducing *NAAP* in the plots. Thus, the model appears to be stable suggesting errors accumulating in the model calculations are not increasing.

Figure 10. Standard deviation of biomass across plots over time for one model run. $NAAP_{\max} = 2719 \text{ g m}^{-2}$, $d = 0.042\text{-}0.01$, and $E = 0.05\text{-}0.3$.

4.3 LMPN recovery times

Recovery times for *NAAP* in the LMPN ranged from 62 and 206 years for $E = 0.3$, 77 to 394 years for $E = 0.2$, 88 to 665 years for $E = 0.15$, and 133 to 1902 years for $E = 0.1$. Table 8 provides these ranges, E , mean and standard deviations. For comparison, *Parkinsonia microphylla*, a tree in the North American desert southwest, was calculated

by Shreve (1917) as 1.6% seedling survival from germination. *MAP* at this study site near Tucson, Arizona is approximately 300 mm yr⁻¹. *MAP* ranges for the LMPN are estimated at 846 – 117 mm yr⁻¹ (Retallack, 2007).

Table 8. Results of the ERM with respect to the four *E*. Corresponding MRT ranges, medians, means, and standard deviations at 100 runs each are shown increasing as *E* decreases. All other parameters remain the same.

<i>E</i> (yr ⁻¹)	Range (yr)	Median (yr)	Mean (yr)	Std. Dev. (yr)
0.30	62 - 206	87	98.33	32.74
0.20	77 - 394	136	148.71	62.39
0.15	88 - 665	224	260.60	145.49
0.10	133 - 1902	492	600.22	391.85

4.4 Speciation model output

The cumulative probability of speciation *S* increases with increasing number of substitutions *K* (Figure 11). Additionally, *S* increases with increasing probability of incompatibility *p_n*. Waiting time to speciation *t_S* calculated for the number of incompatibilities for reproductive isolation *Q* = 18, 20 and *Q* = 29, 31 with *p_n* = 10⁻⁴ and *p_n* = 10⁻⁶, respectively. A range of *Q*'s is used for purposes of providing flexibility of the estimates slightly less than and greater than when *S* first equals 1. Each *t_S* estimated at each *p_n* is also calculated for substitution rates *w* = 4.19×10⁻⁵ and 9.09×10⁻⁵ (Table 9; human and house mouse substitution rates, respectively). Additionally, estimates for a 3.1 increase in evolutionary rates of island taxa from Millien (2006) are presented also. At *p_n* = 10⁻⁴ minimum times for speciation *min(t_S)* appear to range approximately from 100,000 – 230,000 years from Equation 2 (Section 3.7) while taking a 3.1 increase in evolutionary rates for isolated taxa gives and approximate *min(t_S)* range of 33,000 – 75,000 years.

Figure 11. Cumulative probability of speciation S with respect to K substitutions. S is plotted with $p_n = 10^{-4}$, 10^{-5} , and 10^{-6} increasing more slowly with respect to K at smaller p_n .

Table 9. Estimates of t_S at $p_n = 10^{-4}$ and 10^{-6} and $w = 4.19 \times 10^{-5}$ and 9.09×10^{-5} for $Q = 18, 20$ and $Q = 29, 31$, respectively. Estimates for t_S with a 3.1 increase in evolutionary rates as reported for fossil island taxa in Millien are also provided.

w (sub yr ⁻¹)	t_S (yrs)			
	$p_n = 10^{-4}$		$p_n = 10^{-6}$	
	$Q = 18$	$Q = 20$	$Q = 29$	$Q = 31$
4.19×10^{-5}	214836	238707	346125	369996
9.09×10^{-5}	98961	109957	159437	170433
$t_S/3.1$				
4.19×10^{-5}	69302	77002	111653	119353
9.09×10^{-5}	31923	35470	51431	54978

4.5 Testing the hypotheses

Comparing speciation (t_S) and recovery times (t_R) generated by the model it is evident the null hypothesis is to be rejected without a need for statistical testing.

Recovery times are short relative to speciation times (Table 10). Therefore, it is unlikely isolated mammal species form new species following large-scale ash-flow deposition in the LMPN (Table 11 and Figure 12).

Figure 12. Comparison of A) a range of mammalian life expectancies spanning the LMPN body mass dual optima to B) the E -based LMPN $NAAP$ recovery times to C) $\min(t_S)$ of mammals belonging to the body mass dual optima with Millien's (2006) 3.1 increase in evolutionary rates to D) $\min(t_S)$ of mammals belonging to the body mass dual optima without a 3.1 increase in evolutionary rates. Mammalian life expectancies calculated from data in Damuth (1982) with the formula $Life\ expectancy\ (yrs) = 0.0963 \pm 0.0753 (Body\ mass\ (g))^{0.3345 \pm 0.0588}$. Different values of E are designated for each associated recovery time range. For $\min(t_S)$, $p_n = 10^{-4}$ and $Q = 18$.

Table 10. Relationships between maximum MRT $\max(t_R)$ for *NAAP* and the minimum time for speciation in small and large mammals $\min(t_S)$ under model conditions as described in Section 3.7. Two $\min(t_S)$ values are shown for small and large mammals. The value in without parentheses are $\min(t_S)$ with respect to a 3.1 increase in evolutionary rates. $\min(t_S)$ values in parentheses are values with this factor removed.

	$\max(t_R)$ (yrs)	$\min(t_S)$ (yrs)	
		Small Mammals	Large Mammals
	1902	31,923 (98,969)	69,302 (214,836)
$\max(t_R)$ (yrs)	=	<	<
Small Mammals	>	=	<
Large Mammals	>	>	=

Table 11. Results of the null (H_0) and alternate (H_1) hypothesis tests as described in Section 2.3.2. H_0 is rejected and H_1 is accepted. Therefore, speciation in mammals takes too long a period of time for large-scale pyroclastic flows to assist in generating new species.

Test		$\min(t_S)$ (yrs)	
		Small Mammals	Large Mammals
H_0	$\max(t_R)$ (yrs)	reject	reject
H_1	$\max(t_R)$ (yrs)	accept	accept

Chapter 5

Discussion

“As my contribution to the fight against the information explosion I have completely excluded those topics about which I have nothing to say regardless of their importance.”

-Richard Levins, 1968

5.1 Recovery

Terrestrial ecological recovery following the deposition of ash-flows can be considered as a transition from a purely abiotic domain to a biotic domain. Whether one considers succession the development of a superorganism (Clements, 1916) or the result of happenstance (Gleason, 1926), recovery on ash-flows is a change from bare ground to a surface (and subsurface) populated with bacteria, protists, plants, fungi, invertebrates, and vertebrates. Moreover, due to the variety of modes and directions in which succession and its respective studies proceeds, a general theory is presently not feasible (Walker and del Moral, 2003). Despite this absence of generality, Schneider and Kay (1992) propose that ecosystems succeed from sere to sere by effectively reducing the equilibrium energy gradient imposed by incoming solar radiation with increased energy capture, energy flow activity, and number of energy and material cycles. The authors observe this in radiative measurements from a thermal infrared multispectral scanner of different ecosystem types in the H.J. Andrews Experimental Forest, halfway between Sisters and Sweet Home, Oregon in the Cascade Range. Measurements taken from a quarry, clear-cut, Douglas fir plantation, natural forest, and 400 year old Douglas fir forest indicate a reduction of the surface temperature and an increase in the net radiation

flux absorbed at the surface. This approach, at the very least, may serve as a baseline for a theory of succession among all living kingdoms.

5.2 Timing

A relevant question to this report is: what is the appropriate determination for the timing of recovery? As mentioned in Assumption 8 of Section 3.2., this report indicates recovery occurs when 90% of the biomass per plot has accumulated. In modern settings the timing of recovery within a range of climates is generally over hundreds of years. However, the measure of recovery estimated across assorted studies can itself be different furnishing varied recovery times. Additionally, matters of scale (temporal or spatial) regarding experiments and experimental environment (i.e. field, lab, greenhouse, or software) may decide what feature of the recovery process will be measured. Table 14 organizes the general locations, disturbance types, environments, recovery times, and measures used to indicate recovery or present stage. Mostly, recovery times given by these accounts are relatively congruent with one another. They may also fit criteria for generating correlations with climate variables like temperature and precipitation, but more data are needed and the data present are likely not enough to form a sensible relationship.

Regarding congruence of recovery times, early stages of succession appear to qualitatively align. For instance, Chapin et al. (1994) describe a succession of seres following deglaciation at Glacier Bay, Alaska as “Pioneer” in the first 20 years, dominated by dryas after 30 years, dominated by alder after 50 years, and later dominated by spruce after 100 years. Meanwhile, in northcentral Colorado at the Central Plains

Experimental Range (CPER), a shortgrass community was dominated by *Bouteloua gracilis* after 50 years on abandoned agricultural fields (Coffin and Laurenroth, 1990). At Glacier Bay, the glacial till unveiled by the melting glacier sets the ecological landscape back to zero in a biome dominated by spruce trees, whereas in the CPER the landscape is dominated by grasses which are faster growing, shorter lived plants.

Table 12. Different regional studies of succession and their disturbances, environments, recovery times, and measures of recovery.

Location	Disturbance	Environment	Recovery Time (yrs)	Measure	Source
Montagne Pelée, Martinique	nuée ardentes	Tropical Forest	60	Return of vascular plants	Beard, 1976
Rakata Is., Sunda Straits, Indonesia	Krakatau eruption and caldera collapse	Tropical Forest	>100	Number of species	Whittaker et al., 1989
Northcentral Colorado	Fire, grazing	Semiarid Grassland	20 - 65	90% biomass from computational model with validation	Coffin and Laurenroth, 1990
Glacier bay, Alaska	Glacier	Glacial Till	100 -200	Spruce arrival	Chapin, III et al., 1994
North Island, New Zealand	Taupo ash-flow	Temperate Forest	120 - 225	Trace Pteridium spore and charcoal levels/C ¹⁴ dating	Wilmschurst and McGlone, 1996
Grand Canyon, Arizona	Debris flows	Desert Alluvial Fans	240 - 285	% cover of long-lived plants/C ¹⁴ dating	Bowers et al., 1997
Sonoran Desert, Arizona	Man-made	Desert	>78	No. of species, no. of plants, % cover	Guo, 2004
Central and southest Montana	Fire	Shrub Steppe	625	% sagebrush canopy	Cooper et al., 2007

Recovery on Mount St. Helens has been studied since its face-changing eruption on May 18, 1980. However, it is still relatively unknown when it will be fully recovered. Crisafulli et al. (2005b) indicate in their Figure 20.3 the forest system response may return to its pre-eruptive productivity levels in 100 years. By 2005, the lupine pioneer species on the Pumice Plain immediately north of St. Helens had given way to competitors (*Agrostis*, *Hypochaeris*, and *Polytrichum*; del Moral and Lacher, 2005). This is consistent with Glacier Bay's "Pioneer" stage timeline of 20 years. If this rate of recovery continues at Mount St. Helens, perhaps the ecosystem will have made a full recovery in 100 years.

In ancient settings, climate change-induced succession has been well documented (Graham and Grimm, 1990; Overpeck et al., 1992). However, less is known regarding post-disturbance succession in the framework of paleoecology, especially from volcanic activity. Furthermore, from the succession patterns that are inferred from the rock record, fine-scale detail of their timing is difficult to observe.

Taggart and Cross (1974, 1990; and Cross and Taggart, 1982) suggest patterns of change from pollen and plant macrofossil assemblages from the Sucker Creek Formation (15.46-14.77 Ma; Downing and Swisher, 1993) indicate succession instigated by volcanic activity, fire, and climate. Succession is inferred from the assemblages themselves and numerous volcanic deposits in the stratigraphic sections they sampled and measured. Cross and Taggart (1982) estimate, provided no diastems break the sequences, these sections were generally deposited within 10,000 years.

Bubnoff units B (1×10^{-6} m/yr) were used by Cross and Taggart (1982) to estimate deposition times for fluvial (86,000 B) and lacustrine (5,800 B) systems. Some

sandstones units were 6-9 m thick giving approximate deposition time estimates of 70-105 years while 3 m of lignitic shale is estimated to be deposited in roughly 525 years. Nonetheless, no recovery times were given for suspected successions of any of the described associations from any of the deposits. In spite of all these estimates, at least regarding plant macrofossils, Burnham et al. (1992) suggest they are typically deposited in a single year immediately around the locality of deposition.

5.3 Speciation

Examples specifically relating mammalian evolutionary responses to volcanic eruptions are few (e.g. Louys, 2007; Louys et al., 2007). More data and hypotheses exist on mammalian ecological responses instead (Taggart and Cross, 1990; Crisafulli et al., 2005a; Hanser and Huntley, 2006).

Better demonstrations of evolutionary responses are found in terrestrial invertebrate studies concerning the result of the effects of volcanic eruptions on allopatric speciation (Carson and Templeton, 1984; Morgan-Richards et al., 2000; Vandergast et al., 2004). The closest example to the mammalian dichopatric speciation-ash-flow eruption scenario is from changes in weta beetles following the Taupo eruption. Morgan-Richards et al. (2000) suggest the weta *Hemideina thoracica* on the North Island of New Zealand dispersed across the Taupo ash-flow surface at a minimum of 100 m/generation (one generation is ~2 years). Furthermore, differences between populations sampled along the eastern shore of Lake Taupo indicate hybridization of four clines over a distance of 38 km; the result being secondary contact of allopatrically divergent

populations that differentiated following the eruption. It is presumed the clines of *H. thoracica* will become homogenized over time.

To understand timing of speciation in mammals, one of the shortest intervals from the fossil record is 1000 years. From 5000-4000 ka, MacDonald (1981) suggests anagenesis likely occurred from *Bison antiquus antiquus* to *B. bison bison*. However, MacDonald (1981) also suggests *B. antiquus occidentalis* could be an intermediate from 10,000-4000 ka. Despite this short interval, speciation is not in response to ash-flow eruptions. However, the potential 1000 year *B. bison* speciation interval is less than the maximum recovery time of 1902 years computed with $E = 0.1$.

In addition to few data on mammalian evolutionary responses to volcanic eruptions, there may not even be an indirect affect of eruptions on mammalian speciation. Cathers et al. (2010) have recently reported a correlation between Cenozoic climate changes with ash-flow eruption volumes in western North America. However, studies and reviews of the relationship between climate and mammalian extinction and speciation indicate this matter to be unresolved (Prothero, 1999, 2004; Alroy et al., 2000; van Dam et al., 2006; Louys, 2007). It may well be that mammal populations form new species more readily from active processes such as competition and foraging-driven or density-dependent dispersal than the passive processes of happenstance or directional environmental change. Additionally, Taggart and Cross (1990) demonstrate a specific case of a grazing fauna collected within sediments that contain pollen assemblages representing post-eruption successional grass-forb associations. If grasses could be established and widespread in a short time after the eruption of these large-scale ash-flows, perhaps isolated populations of grazing mammals and their associated taxa would

reunite well in advance of speciation. Moreover, vegetated “oases” of plant associations other than grasses and forbs may not be accessible to all members of nearby communities due to a lack of adequate resources at, or en route to, such sites. Passage may be eased by grasses better than ash surfaces alone. Since small mammals have demonstrated their capacity to locate, find adequate forage in, and inhabit oases on the pyroclastic flow of Mount St. Helens (Crisafulli et al., 2005a)—a greatly reduced example in magnitude—widespread grasses may possibly unite isolated populations of non-grazers in a short time as well by island hopping along oases.

5.4 ERM dynamics

Decreasing *MAP* decreases maximum *NAAP* and *FVC* (i.e. biomass carrying capacity and maximum vegetation cover, respectively). However, leaving *d* and *E* unchanged generates shorter recovery times. This is unrealistic because *FVC* gives a measure of the success and extent seedlings have in different climates. Therefore, in the case of recovery times in different climates tuning *E* was required to determine an adequate calibration of the model before examining the LMPN recovery times. Tuning *d* was not required since there was some data available to use in the simulations.

Concerning variability between the model runs, there is considerable contingency based on the stochastic nature of *d* and *E*. A decrease in *E* causes *d* to have a greater influence over the trajectory in the timing of ecosystem and per plot biomass recovery. The same can be said if *d* were decreased instead. Such a role for stochasticity and contingency in the ERM is analogous to Gould’s (1989) description of contingency in the history of life on Earth. Rewinding the tape recorder of life and recording over the last

recording will record a different evolutionary outcome. Though some MRT output are the same, how the plots developed are not.

5.5 Coda for ERM limitations

Limitations of the ERM remain data deficiencies with their associated uncertainty. In addition to this primary issue is the choice of model. With more data the ERM is likely to change from allometric and regression equations and simple rule based algorithms to more accurate rules or numerical solutions in models described in Section 3.2.1. At this time further data mining, experiment, and validation is needed to increase the realism of the model.

5.6 Future work

Future work should establish better estimates of E and d . This could be done in the literature in conjunction with direct contact with ecologists studying succession and their associated ecosystem dynamics. Additionally, experiments which determine the affects of root inhibition in ash for pioneer plant species and species interactions in later stages would improve understanding of competition processes. Pollen rich outcrops or sediment cores with any of the three LMPN large ash-flow tuffs at their base are ideal such as those sampled and measured by Wilmshurst and McGlone (1996). Such a discovery would provide interpretation of actual events. This would aid in guiding the modeling of the processes in the LMPN to match preserved patterns. Finally, analyses of the ERM itself will generate a better knowledge on its quality. Sensitivity analyses of the

parameters and variables, stability analyses for understanding model output error, and uncertainty analyses of parameter error are all potential directions to explore.

Chapter 6

Conclusions

The purpose of this thesis is to explore the potential for speciation in mammals following the eruption of large-scale ash-flow tuffs in the LMPN. To accomplish this initial exploration of the dynamics in ecosystem recovery were studied and implemented in the ERM. The intent was to form an approximate answer to the question of mammalian evolutionary responses to extensive volcanic phenomena.

Unlike other models equipped to study ecological recovery, the ERM here uses general relationships between the biotic and abiotic domains to establish recovery times rather than apply site and/or species-specific characteristics of either domain. In effect, all one needs is a precipitation range, along with estimates of disturbance and seedling establishment rates and the model is essentially set to proceed. More importantly, this quality makes it applicable to terrestrial paleoecological studies with similar coarseness in data. The strength of the model comes from its heavy reliance on empirical relationships or other observations found in the literature. By this account, it should broadly reflect much of the present state of knowledge on ecological recovery and interactions between organisms with each other and their environment. As indicated through validation in Section 4.1 (Table 5), the ERM generates a distribution statistically indiscernible from the distribution of ORT data following the Taupo eruption (Wilmshurst and McGlone, 1996).

Despite all efforts made in generating the ERM, results of its recovery time output—as compared to Orr’s (1995) and Orr and Turreli’s (2001) models of speciation and the literature—prove to be too short for populations of mammals to speciate upon

becoming isolated. Under these circumstances, following such extreme events as large-scale ash-flow eruptions in the LMPN, potential for speciation in mammals is unlikely.

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Appendix A. Creation of Figure 1

Patterns

Mammals are the chosen fossils to study and indicate changes in the ecosystems of the PNW (and more specifically the LMPN) since they are best preserved, most diverse, and most abundant. The data come from outcrops in formations ranging 45 – 0.01 Ma within a 400 km radius of the proposed caldera source for the RST near Capehart Lake, Oregon (Streck and Grunder, 1995).

Data collection

In order to reach a better understanding of the patterns of the temporal ranges of mammal species, data collection from multiple sources was conducted. Taxonomic range maps are typically generated with successive taxa on one axis and their temporal ranges on a second axis. However, in order to distinguish species as more than Latin nomenclature their physical attribute of mass was collected for one axis because of several revealing biases (e.g. sampling, preservation, genetic variation, and reproductive) it affords. Collecting data on body masses is tedious work since much data can be scattered or the regression and allometric equations used to estimate mass are locked away in obscure publications and isolated from one another. Methods of data collection were to gather body mass data 1) from the Paleobiology Database's North American Fossil Mammal Systematics Database (NAFMSD) and publications (e.g. see MacFadden and Hulbert, 1990 and Christiansen, 2004), or 2) calculate estimates of mass from tooth measurements on a specific taxon from the NAFMSD, Janis et al. (1998), or Janis et al. (2008) using regression or allometric equations (Table A.1) for the lowest possible

classification (class, order, family) from publications such as Legendre (1986), Legendre and Roth (1988), Damuth (1990), Janis (1990), Alroy (1998b, 1999), Bloch et al. (1998), or 3) average the mass from a range of data on a taxon's genus from the NAFMSD or Silva and Downing (1995) on genera at masses above 18 g (Smith et al., 2004). The third method was rarely required and species belonging to genera less than 18 g requiring this step were not encountered. Actual data are presented in Table A.3.

Table A.1. Prediction equations for mammalian body mass (g) from lower first molar tooth (mm) measurements.

Group	Prediction Equation	Reference
All Mammals	$\ln(B_M) = 1.827 \cdot \ln(m_1 \text{ area}) + 1.81$	Legendre, 1986
Carnivora	$\ln(B_M) = 1.897 \cdot \ln(m_1 \text{ area}) + 1.653$	Legendre and Roth, 1988
Canidae	$\ln(B_M) = 2.815 \cdot \ln(m_1 \text{ area}) + 1.337$	Legendre and Roth, 1988
Felidae	$\ln(B_M) = 2.951 \cdot \ln(m_1 \text{ area}) + 1.535$	Legendre and Roth, 1988
Ursidae	$\ln(B_M) = 2.033 \cdot \ln(m_1 \text{ area}) + 1.886$	Legendre and Roth, 1988
Mustelidae	$\ln(B_M) = 1.374 \cdot \ln(m_1 \text{ area}) + 1.649$	Legendre and Roth, 1988
Non-selenodont Ungulates	$\log(B_M) = 3.12 \cdot \log(p_4 - m_2 \text{ length}) - 0.43$	Damuth, 1990
All Ungulates	$\ln(B_M) = 3.263 \cdot \ln(m_1 \text{ area}) + 1.337$	Janis, 1990
Perissodactyla	$\ln(B_M) = 3.187 \cdot \ln(m_1 \text{ area}) + 1.264$	Janis, 1990
Rodentia	$\ln(B_M) = 1.767 \cdot \ln(m_1 \text{ area}) + 3.267$	Legendre, 1986
Lipotyphla	$\ln(B_M) = 1.714 \cdot \ln(m_1 \text{ area}) + 0.886$	Bloch et al., 1998
Primates	$\ln(B_M) = 1.49 \cdot \ln(m_1 \text{ area}) + 3.577$	Legendre, 1986

Collecting data on species and their temporal ranges was done with the NAFMSD, Carrasco et al. (2005; “MIOMAP”), Janis et al. (1998), or Janis et al. (2008). However, corrections were made on temporal ranges of taxa from literature using the temporal ranges of formations (Table AI.2). Rather than use the North American Land Mammal Ages (NALMA) of Tedford et al. (2004) or the revised quantitative NALMA time scale of Alroy (2003), temporal ranges of formations and outcrops are used instead since many of the temporo-stratigraphic benchmarks, tie points, and stratigraphic applications (i.e. dated tuffs and paleomagnetism) used by these authors are not up to date (e.g. re: RST and DvCT). The unfortunate part of this is that the temporal resolution of species ranges has the potential to decrease dramatically since a species may actually become regionally extinct below the upper-most dated horizon of a formation or may first occur somewhere above. For example, this is true in my experience regarding less common taxa in outcrops of the John Day Formation. Hence, one could argue that since the resolution of the data is so low that the pattern cannot be completely understood and therefore, the test of the pattern does not fulfill its promise. However, viewing the data at the outcrop scale is a more precise endeavor than applying ranges to species based on a qualitative or quantitative NALMA since the focus is on more restricted areas and temporal data are up to date. Moreover, nearly all the fossiliferous formations in the LMPN are much shorter in duration than the John Day Formation (a Miocene average of approximately a little less than four million years/formation or basin ($n = 17$) compared to the approximate 20 million years of the John Day Formation). Therefore, in this case, NALMA's are far lower in their resolution despite their advantages of correlation across greater spatial scales.

Table A.2. Formations and their temporal durations as determined by their references.

Formation	Age Range	Reference
Deschutes Fm.	7.6 - 4 Ma	Smith, 1986
Chenoweth Fm.	7.5 - 5.1 Ma	Farooqui et al., 1981
Tygh Valley Fm.	7.4 - 4.9 Ma	Farooqui et al., 1981
Alkali Canyon Fm.	< 10.5 Ma	Farooqui et al., 1981
McKay Fm.	< 14 Ma; 10 - 4.5 Ma	Bergerren and van Couvering, 1974; Farooqui et al., 1981
John Day Fm.	39.72 - ~20 Ma	Retallack et al., 1996 Fremd et al., 1994
Clarno Fm.	53.5 - 43.4 Ma	Bestland et al., 1999
Ellensberg Fm.	17 - ~5 Ma	Smith, 1988
Ringold Fm.	8.5 - 3.4 Ma	Fecht et al., 1987
Mascall Fm.	~16 - 14.8 Ma	Prothero et al., 2006a;
Rattlesnake Fm.	7.5 - 6.9 Ma	Retallack et al., 2002; Retallack, writ comm, 2008; Prothero et al., 2006b
Drewsey Fm.	9.68 - 6.9 Ma	Johnson et al., 1996; Retallack 2004; Camp et al. 2003
Juntura Fm.	~10.9 - 9.68 Ma	Kohn and Law, 2006
Ironside Fm.	12.4 - 9.68 Ma	Everenden and James, 1964*; Johnson et al., 1996; Retallack, 2004
Deer Butte Fm.	15 - 12.6 Ma	Cummings, 1991
Butte Creek Volcanic Sandstone Fm.	~15.8 - 15.5 Ma?	Everenden and James, 1964*; Evans, 1990; Swisher, 1992
Sucker Creek Fm.	>15.46 - <14.77 Ma	Downing 1992; Downing and Swisher 1993;

Table A.2. continued

Chalk Butte Fm.	< 10.18 Ma - ~ 3 Ma	Hart, 1982*; Cummings et al., 2000; Kimmel, 1982 (and references therein)
Chalk Hills Fm.	8.9 - 6.6 Ma	Kimmel, 1982; Beranek et al., 2006
Glens Ferry Fm.	5 - 3 Ma	Beranek et al., 2006
Starlight Fm.	~> 10.2 - ~> 6.2 Ma	Kellogg et al., 1994
Humboldt Fm.	15.54 - 9.81 Ma	Perkins et al., 1998
Virgin Valley Fm.	>16.28 - <15.18 Ma	Perkins et al., 1998
Thousand Creek Fm.	8.3 - 7.02 Ma	Perkins et al., 1998; Prothero and Davis, 2008
Lake Idaho	9.5 - 2.5 Ma	Beranek et al., 2006
Harney Basin	9.68 - 7.05 Ma	Sheppard, 1995 [modified]

* Corrected using Dalrymple (1979)

State of the mammalian fossil record: small mammals vs. large mammals

A number of biases can affect the study of fossil organisms. For fossil mammals these include: collecting biases for size or taxonomic group (Lyman, 1984; Retallack, 1988; Behrensmeyer et al., 2000) due to visibility or preservation biases, naming biases for size or taxonomic group (Alroy, 2003) due to worker preferences or competitive inclination (e.g. O.C. Marsh and E.D. Cope's late 19th century naming feud), debate biases for taxonomic nomenclature (Alroy, 2003) due to synonymous or dubious names, and preservation biases for size (Behrensmeyer et al., 1979; Behrensmeyer, 1988;

Retallack, 1988; Foote and Raup, 1996; see also Sections 2.1.1 and 2.1.2 in main body of text for further explanations) due to physical and chemical destruction of organic remains, the negative correlation of abundance with size, or the positive correlation of abundance with preservation.

With all these biases it is difficult to know what to account for when regarding numbers of taxa in different categories such as size or taxonomic group. Section 2.1.1 expands on this topic regarding inherent qualities in taxa that influence their presence in the fossil record. Section 2.1.3 illustrates what the pattern or size distributions may indicate. Additionally, below is a short summary of the potential role climate has on diversity as filtered through the fossil record and different size groups.

Recent studies on the consequences of climate on mammalian diversity and turnover through time have generated opposing observations and they have led to different interpretations of climate effects on evolution in mammals. This, in turn, perhaps influences diversity biases which will affect species abundance, geographic extent, and lifespan (see Section 2.1.1). Results for one study (van Dam et al., 2006) explains small mammal species life spans are determined by orbital eccentricity cycle minima (2.37 Ma) and obliquity cycle nodes (1.2 Ma) which correspond to mean mammalian life spans (2.5 Ma; Alroy, 2000). Hence, at these orbital cycles small mammal diversity turns over—at least in the Neogene (24-2 Ma) fluvio-lacustrine sections in the Madrid, Calatayud-Daroca and Teruel basins from central Spain. Meanwhile, results of another study (Liow et al., 2008) using the Neogene Old World (NOW) fossil mammal database have indicated that large mammals turnover more rapidly than small mammals. The authors of this report cite multiple reasons for this

pattern in large mammals. Examples include more frequent deleterious mutations, smaller population sizes, longer generation times, and a low frequency in sleep-or-hide behavior (SLOH; e.g., hibernation, torpor, and burrowing). Despite these research efforts, Barry et al. (2002) could only find partial qualitative evidence for turnover events in large mammals related to environmental (e.g., fluvial and vegetation) or climate change in the Siwalik formations of the Potwar Plateau of northern Pakistan. Finding partial qualitative evidence for turnover is diminished somewhat by the efforts of the more quantitative studies put forth recently (as mentioned above) and most likely in the near future. Furthermore, a quantitative study (Alroy et al., 2000) indicated no correlation between (mostly western) North American mammal diversity changes and Atlantic benthic foraminiferal oxygen isotope ratios over the same time period. However, one could argue these records are at the opposite ends of any potential number of energy and mass transfer pathways within Earth's global surficial system. How is one to know when, where, or how along the way from global temperature—proxied by oxygen isotopes—to ecosystem diversity dynamics, the initial temperature signal was strong, lost, or scattered before it reached ecological communities and their accompanying populations? Alroy et al. (2000) briefly touched on a similar impression while mostly making their argument against a direct correlation between global temperature and western North American mammalian diversity and turnover.

Table A.3. Cenozoic PNW mammalian mass, first occurrence (FO), and last occurrence (LO) data mined from collections in an ~500,000 km² area centered on Harney Basin, Oregon. Data sorted oldest to youngest by LO.

Taxon	mass (g)	FO (Ma)	LO (Ma)	notes/comments
<i>Hyrachyus eximius</i>	87400	44.10	43.70	
<i>Patriofelis ferox</i>	22418	44.10	43.70	mass from P. ultra
<i>Telmatherium</i> sp.	420250	44.10	43.70	mass from mean of known estimates in genus
<i>Xenicohippus craspedotus</i>	10895	44.10	43.70	mass from mean of known estimates in genus
<i>Achaenodon fremdi</i>	774100	43.70	39.70	mass from A. robustus
<i>Epihippus gracilis</i>	7800	43.70	39.70	
<i>Haplohippus texanus</i>	13800	43.70	39.70	
<i>Hemipsalodon grandis</i>		43.70	39.70	
<i>Heptacodon</i> sp.	127600	43.70	39.70	
<i>Plesiocolopirus hancocki</i>	23700	43.70	39.70	
<i>Procadurcodon</i> sp.		43.70	39.70	
<i>Protitanops curryi</i>	1424775	43.70	39.70	mass guesstimated as 3/4 the mass of Brontops based on comparisons of M2 lengths.
<i>Teletaceras radinskyi</i>	91600	43.70	39.70	
<i>Colodon</i> sp.	49980	39.70	37.50	mass from mean of known estimates in genus
<i>Mesohippus bairdi</i>	22000	32.90	32.60	
<i>Subhyracodon</i> sp.	159900	32.90	32.60	mass from mean of known estimates in genus
<i>Diceratherium</i> sp.	515780	30.28	30.00	mass from mean of known estimates in genus
<i>Agriochoerus</i> sp.	63850	43.70	29.73	mass from mean of known estimates in genus
<i>Archaeocyon pavidus</i>	902	30.00	29.73	
<i>Enhydrocyon</i> sp.	24280	30.00	29.73	mass from mean of known estimates in genus
<i>Eusmilus cerebrealis</i>		30.00	29.73	
<i>Perchoerus</i> sp.	60733	30.00	29.73	mass from mean of known estimates in genus
<i>Temnocyon altigenis</i>	19300	30.00	29.73	
<i>Thinohyus lentus</i>	101400	30.00	29.73	
<i>Allocyon loganensis</i>		30.00	28.90	
<i>Archaeolagus ennisianus</i>	198	29.45	28.70	
<i>Cynarctoides lemur</i>	1020	30.00	28.70	

Table A.3 continued.

<i>Dinaelurus crassus</i>	37320	29.45	28.70	
<i>Dinictis cyclops</i>		29.45	28.70	
<i>Enhydrocyon stenocephalus</i>	22100	29.45	28.70	
<i>Haplomys liolophus</i>	39	30.00	28.70	mass from <i>H. galbreathi</i>
<i>Leptocyon mollis</i>	3300	29.45	28.70	mass from mean of known estimates in genus
<i>Merycoidodon bullatus</i>	109500	29.45	28.70	
<i>Mesocyon coryphaeus</i>	10400	29.45	28.70	
<i>Mesocyon sp.</i>	7618	29.45	28.70	mass from mean of known estimates in genus
<i>Micropternodus morgani</i>	72	29.45	28.70	
<i>Miohippus anceps</i>	41650	29.45	28.70	mass from mean of known estimates in genus
<i>Miohippus condoni</i>	41650	29.45	28.70	mass from mean of known estimates in genus
<i>Miohippus equiceps</i>	41650	29.45	28.70	mass from mean of known estimates in genus
<i>Miosciurus balloviensis</i>	37	29.45	28.70	
<i>Osbornodon sesnoni</i>	7430	29.45	28.70	
<i>Palaeocastor peninsulatus</i>	947	29.45	28.70	mass from mean of known estimates in genus
<i>Phlaocyon latidens</i>	1580	30.00	28.70	
<i>Pogonodon platycopis</i>	31200	29.45	28.70	mass from <i>P. eileenae</i>
<i>Allomys simplicidens</i>	122	28.70	27.50	mass from mean of known estimates in genus
<i>Alwoodia magna</i>	226	28.70	27.50	mass from <i>A. harkseni</i> m1 area
<i>Capacikala gradatus</i>		28.70	27.50	
<i>Desmatochoerus megalodon</i>	335100	28.70	27.50	
<i>Diceratherium armatum</i>	1250100	32.90	27.50	
<i>Hypertragulus hesperius</i>	4572	30.00	27.50	
<i>Jimomys lulli</i>	28	28.70	27.50	
<i>Meniscomys uhtoffi</i>	70	28.70	27.50	mass from <i>M. hippodus</i>
<i>Mesoreodon minor</i>	159700	28.70	27.50	
<i>Miohippus intermedius</i>	43000	28.70	27.50	
<i>Nimravus brachyops</i>	52604	30.00	27.50	
<i>Pleurolicus sulcifrons</i>	84	28.70	27.50	

Table A.3 continued.

<i>Allomys sp.</i>	122	27.50	25.30	mass from mean of known estimates in genus
<i>Cormocyon copei</i>	3210	29.45	25.30	
<i>Daphoenus sp.</i>	7919	30.00	25.30	mass from mean of known estimates in genus
<i>Diceratherium annectens</i>	227800	30.00	25.30	mass estimated from M3 length
<i>Ekgmowechashala sp.</i>	1085	27.50	25.30	
<i>Entoptychus basilaris</i>	84	27.50	25.30	mass from mean of known estimates in genus
<i>Eporeodon occidentalis</i>	118300	30.00	25.30	
<i>Gentilicamelus sternbergi</i>	77400	27.50	25.30	
<i>Merycoidodon major</i>	62200	28.70	25.30	
<i>Mesocyon brachyops</i>	7040	29.45	25.30	
<i>Miohippus sp.</i>	41650	30.28	25.30	mass from mean of known estimates in genus
<i>Oreodontoides oregonensis</i>	34900	28.70	25.30	
<i>Oreodontoides sp.</i>	34900	28.70	25.30	mass from <i>O. oregonensis</i>
<i>Paraenhydrocyon josephi</i>	6670	30.00	25.30	
<i>Pogonodon n. sp.</i>	15600	27.50	25.30	apparent dwarfed new Pogonodon species guesstimated here at half <i>P. eileenae</i> 's mass
<i>Protospermophilus vortmani</i>	230	28.70	25.30	
<i>Agriochoerus guyotianus</i>	59000	32.90	23.80	
<i>Archaeotherium sp.</i>	2109817	32.90	23.80	mass from mean of known estimates in genus
<i>Entoptychus cavifrons</i>	70	25.30	23.80	
<i>Entoptychus minor</i>	84	25.30	23.80	mass from mean of known estimates in genus
<i>Entoptychus productidens</i>	84	25.30	23.80	mass from mean of known estimates in genus
<i>Entoptychus transitorius</i>	84	25.30	23.80	mass from mean of known estimates in genus
<i>Entoptychus wheelerensis</i>	84	27.50	23.80	mass from mean of known estimates in genus
<i>Hypertragulus calcaratus</i>	8880	27.50	23.80	
<i>Kalobatippus praestans</i>		25.30	23.80	
<i>Leidymys nematodon</i>	38	25.30	23.80	mass from mean of known estimates in genus
<i>Meniscomys hippodus</i>	70	27.50	23.80	
<i>Merycochoerus superbus</i>	438400	27.50	23.80	

Table A.3 continued.

<i>Merycoides pariogonus</i>	77000	27.50	23.80	
<i>Micropternodus</i> sp.	71	25.30	23.80	mass from mean of known estimates in genus
<i>Miohippus primus</i>	41650	25.30	23.80	mass from mean of known estimates in genus
<i>Nanotragulus planiceps</i>	3678	29.45	23.80	mass from mean of known estimates in genus
<i>Oligobunis crassivultus</i>	13000	25.30	23.80	mass from <i>O. floridanus</i>
<i>Palaeolagus</i> sp.	161	27.50	23.80	mass from mean of known estimates in genus
<i>Palustrimus lewisi</i>	84	25.30	23.80	mass from mean of known estimates in genus; i.e. <i>Entoptychus</i>
<i>Paroreodon parvus</i>	51150	27.50	23.80	
<i>Proheteromys thorpei</i>	16	25.30	23.80	
<i>Protosciurus condoni</i>	629	25.30	23.80	
<i>Rhizocyon oregonensis</i>	1570	30.00	23.80	
<i>Schizodontomys sulcidens</i>	65	25.30	23.80	
<i>Daphoenodon</i> sp.	45000	25.30	23.20	mass from mean of known estimates in genus
<i>Daphoenus socialis</i>	13000	25.30	23.20	
<i>Entoptychus planifrons</i>	135	25.30	23.20	
<i>Hypsiops breviceps</i>	230500	29.45	23.20	
<i>Merycochoerus matthewi</i>	448333	23.80	23.20	mass from mean of known estimates in genus
<i>Merycoides longiceps</i>	108633	23.80	23.20	
<i>Paradaphoenus</i> sp.	2040	23.80	23.20	mass from mean of known estimates in genus
<i>Rudiomys mcgrewi</i>		23.80	23.20	
<i>Schizodontomys greeni</i>	94	23.80	23.20	mass from mean of known estimates in genus
<i>Merycochoerus</i> sp.	448333	22.00	19.60	mass from mean of known estimates in genus
<i>Miotapirus</i> sp.	71400	23.20	19.60	mass from <i>M. harrisonensis</i>
<i>Moropus oregonensis</i>	90300	25.30	19.60	
<i>Archaeohippus</i> sp.	26571	22.00	19.00	mass from mean of known estimates in genus
<i>Archaeolagus macrocephalus</i>	374	23.80	19.00	
<i>Entoptychus individens</i>	84	25.30	19.00	mass from mean of known estimates in genus
<i>Hypertragulus</i> sp.	10423	30.28	19.00	mass from mean of known estimates in genus
<i>Merychys arenarum</i>	75000	23.80	19.00	

Table A.3 continued.

<i>Merychys minimus</i>	41200	22.00	19.00	
<i>Nexuotapirus robustus</i>	138200	25.30	19.00	
<i>Palaeocastor sp.?</i>	947	22.00	19.00	mass from mean of known estimates in genus
<i>Parahippus leonensis</i>	48700	22.00	19.00	
<i>Alphagaulus vetus</i>	521	16.58	16.47	
<i>Ansomys nevadensis</i>	52	16.58	16.47	
<i>Bassaricyonoides stewartae</i>	1700	16.58	16.47	mass from <i>B. phyllismillerae</i> m1 area
<i>Bouromeryx submilleri</i>	69100	22.00	16.47	
<i>Cynorca sociale</i>	39800	22.00	16.47	
<i>Hesperhys pinensis</i>	246700	16.58	16.47	
<i>Hesperhys vagrans</i>	181000	16.58	16.47	
<i>Limnoecus compressus</i>		16.58	16.47	
<i>Liodontia sp.</i>	198	16.58	16.47	mass from <i>L. alexandrae</i>
<i>Megapeomys bobwilsoni</i>	413	16.58	16.47	
<i>Miospermophilus sp.</i>	84	16.58	16.47	
<i>Miospermophilus wyomingensis</i>	83	16.58	16.47	
<i>Paracosoryx wilsoni</i>		16.58	16.47	
<i>Parapliohippus carrizoensis</i>	42300	16.58	16.47	
<i>Protospermophilus angusticeps</i>	321	16.58	16.47	
<i>Protospermophilus sp.</i>	218	16.58	16.47	mass from mean of known estimates in genus
<i>Subdromomeryx antilopinus</i>		16.58	16.47	
<i>Ursavus brevirohinus</i>		16.58	16.47	
<i>Amphicyon frendens</i>	135600	15.80	15.50	
<i>Bouromeryx americanus</i>	92200	16.58	15.50	
<i>Cynelos sinapius</i>	133000	15.80	15.50	
<i>Euoplocyon brachygnathus</i>	9380	15.80	15.50	
<i>Hesperogaulus gazini</i>		15.80	15.50	
<i>Lanthanotherium sp.</i>	91	15.80	15.50	mass from <i>L. sawini</i>

Table A.3 continued.

<i>Limnoecus sp.</i>	5	15.80	15.50	some taxa in genus have mass below 18g; however, there are real m1 length and width measurements for " <i>L. sp.</i> "
<i>Martes gazini</i>	1767	15.80	15.50	mass from mean of known estimates in genus
<i>Monosaulax typicus</i>	367	15.80	15.50	
<i>Oreolagus wallacei</i>	77	15.80	15.50	
<i>Paradomnina relictus</i>	24	15.80	15.50	
<i>Parahippus pawniensis</i>	51100	16.58	15.50	
<i>Paratomarctus temerarius</i>	11100	15.80	15.50	
<i>Petauristodon sp.</i>		15.80	15.50	
<i>Pliocyon medius</i>	105700	15.80	15.50	
<i>Protospermophilus malheurensis</i>	103	15.80	15.50	
<i>Pseudotrimylus mawbyi</i>	142	15.80	15.50	
<i>Pseudotrimylus sp.</i>	142	16.58	15.50	mass from <i>P. mawbyi</i>
<i>Scapanoscapter simplicidens</i>	59	15.80	15.50	
<i>Ticholeptus sp.?</i>	154900	15.80	15.50	mass from <i>T. zygomaticus</i>
<i>Ursavus primaevus</i>		15.80	15.50	
<i>Alphagaulus pristinus</i>	521	15.85	15.18	mass from <i>A. vetus</i> m1 area
<i>Blastomeryx mollis</i>	35700	15.85	15.18	mass from mean of known estimates in genus
<i>Hesperhys sp.</i>	213850	15.85	15.18	mass from mean of known estimates in genus
<i>Hypolagus parviplicatus</i>	323	15.85	15.18	
<i>Liodontia alexandrae</i>	198	15.85	15.18	
<i>Metatomarctus sp. A</i>	10500	15.85	15.18	mass from <i>M. canavus</i>
<i>Monosaulax skinneri</i>	830	15.85	15.18	
<i>Oreolagus nevadensis</i>	78	15.85	15.18	mass from mean of known estimates in genus
<i>Paracosoryx sp.</i>		15.85	15.18	
<i>Paracynarctus kelloggi</i>	8160	16.58	15.18	
<i>Peraceras profectionum</i>	435250	15.85	15.18	mass from mean of two separate estimates on M2 area and M3 length, respectively. Certainty of value unknown.
<i>Probassariscus antiquus (mathewi?)</i>	916	15.85	15.18	

Table A.3 continued.

<i>Protomarctus optatus</i>	11100	16.58	15.18	
<i>Thinohyus</i> sp.	101400	15.85	15.18	mass from <i>T. lentus</i>
<i>Zygodolophodon proavus</i>		15.85	15.18	
<i>Archaeohippus ultimus</i>	26571	15.80	14.80	mass from mean of known estimates in genus
<i>Arctomyoides</i> sp.	1230	15.77	14.80	mass from <i>A. arctomyoides</i> m1 area
<i>Cynorca</i> sp.	44425	15.77	14.80	mass from mean of known estimates in genus
<i>Hypolagus</i> sp.	319	15.77	14.80	mass from mean of known estimates in genus
<i>Leptarctus oregonensis</i>	2580	15.77	14.80	mass from <i>L. primus</i>
<i>Protospermophilus oregonensis</i>	218	15.77	14.80	mass from mean of known estimates in genus
<i>Tephrocyon rurestris</i>	12100	15.80	14.80	
<i>Acritohippus isonensis</i>	67000	15.85	14.77	
<i>Hypohippus osborni</i>	137100	15.85	14.77	
<i>Moropus</i> sp.	173767	16.58	14.77	mass from mean of known estimates in genus
<i>Pseudotheridomys</i> sp.	8	15.46	14.77	mass from <i>P. pagei</i>
<i>Ursavus</i> sp.		30.00	14.77	
<i>Brachycrus</i> sp.	328700	16.12	14.50	
<i>Desmatippus avus</i>	86700	15.85	14.50	
<i>Hypohippus</i> sp.	117775	16.12	14.50	mass from mean of known estimates in genus
<i>Merychippus brevidontus</i>	62200	16.12	14.50	
<i>Merychippus californicus</i>	44700	16.12	14.50	
<i>Merychippus close</i>	60471	16.12	14.50	mass from mean of known estimates in genus
<i>Metatomarctus</i> sp.	10500	16.12	14.50	mass from <i>M. canavus</i>
<i>Moropus merriami</i>	173767	16.12	14.50	mass from mean of known estimates in genus
<i>Paracosoryx nevadensis</i>		16.12	14.50	
<i>Ticholeptus zygomanticus</i>	154900	16.58	14.50	
<i>Ursavus pawniensis</i>		16.12	14.50	
<i>Zygodolophodon</i> sp.		16.58	14.50	
<i>Achlyoscapter longirostris</i>	12	15.80	12.60	
<i>Alluvisorex arcadentes</i>	6	15.80	12.60	

Table A.3 continued.

<i>Copemys barstowensis</i>	27	15.00	12.60	
<i>Copemys pagei</i>	12	15.80	12.60	
<i>Domninoidea sp.</i>	83	15.00	12.60	mass from mean of known estimates in genus
<i>Dromomeryx borealis</i>	278700	15.85	12.60	
<i>Ingentisorex tumididens</i>	89	15.00	12.60	
<i>Leptodontomys quartzi</i>	3	15.00	12.60	
<i>Macrogathomys sp.</i>	5	15.00	12.60	
<i>Merychippus relictus</i>	60471	15.77	12.60	mass from mean of known estimates in genus
<i>Monosaulax progressus</i>	427	15.00	12.60	
<i>Mustela sp.</i>	505	15.00	12.60	mass from mean of known estimates in genus
<i>Mystipterus pacificus</i>	15	15.80	12.60	
<i>Peridiomys oregonensis</i>	28	15.80	12.60	
<i>Plesiosorex donroosai</i>	686	15.80	12.60	
<i>Pseudotheridomys pagei</i>	8	15.80	12.60	
<i>Scalopoides ripafodiator</i>	28	15.80	12.60	
<i>Spermophilus tephros</i>	89	15.80	12.60	
<i>Hoplectis grangerensis</i>	15700	12.00	10.50	
<i>Ammospermophilus junturensis</i>	54	10.57	9.68	
<i>Copemys dentalis</i>	13	10.57	9.68	
<i>Crusafontina minima</i>	14	10.57	9.68	
<i>Cupidinimus sp.</i>	11	10.57	9.68	some taxa in genus have mass below 18g; however, there are real m1 length and width measurements for "C. sp."
<i>Eucastor malheurensis</i>	746	10.57	9.68	
<i>Gomphotherium sp.?</i>	4157231	10.57	9.68	mass from mean of estimates of <i>G. productens</i> (Christiansen, 2004)
<i>Hesperolagomys galbreathi</i>	136	10.57	9.68	
<i>Hesperosorex sp.?</i>		10.57	9.68	
<i>Hypolagus fontinalis</i>	228	15.77	9.68	
<i>Hystriopsis sp.?</i>	2500	10.57	9.68	mass from <i>H. venustus</i>
<i>Leptocyon sp.</i>	3300	10.57	9.68	mass from mean of known estimates in genus

Table A.3 continued.

<i>Mammut furlongi</i>	6310400	10.57	9.68	mass from mean of estimates of <i>M. americanum</i> (Christiansen, 2004)
<i>Megatylopus sp.</i>	1665000	10.57	9.68	mass from mean of known estimates in genus
<i>Merychys sp.</i>	100686	16.58	9.68	mass from mean of known estimates in genus
<i>Mystipterus sp.</i>	15	10.57	9.68	some taxa in genus have mass below 18g; however, there are real m1 length and width measurements for " <i>M. sp.</i> "
<i>Plesiosorex sp.</i>	340	10.57	9.68	mass from mean of known estimates in genus
<i>Procamelus grandis</i>	606800	10.57	9.68	
<i>Scapanus shultzi</i>	97	10.57	9.68	mass from mean of known estimates in genus
<i>Sthenictis juturensis</i>	4740	10.57	9.68	
<i>Tardontia occidentale</i>	186	10.57	9.68	
<i>Sthenictis sp.</i>	5810	10.57	8.90	mass from mean of known estimates in genus
<i>Borophagus pugnator</i>	36100	8.90	8.50	tf is questionable
<i>Pliosaccomys sp.</i>	22	10.57	7.83	mass from mean of known estimates in genus
<i>Aphelops sp.</i>	1170050	16.58	7.02	mass from mean of known estimates in genus
<i>Dinohippus sp.</i>	262840	8.30	7.02	mass from mean of known estimates in genus
<i>Diprionomys minnimus</i>	21	8.30	7.02	
<i>Dromomeryx sp.</i>	278700	15.77	7.02	mass from <i>D. borealis</i> , the only known and validated species in this genus
<i>Hesperogaulus sp.</i>		15.85	7.02	
<i>Hipparion sp.</i>	69300	8.30	7.02	mass from mean of known estimates in genus
<i>Ilingoceros alexandrae</i>		8.30	7.02	
<i>Ilingoceros schizoceros</i>		8.30	7.02	
<i>Mammut matthewi</i>	6310400	8.30	7.02	mass from mean of estimates of <i>M. americanum</i> (Christiansen, 2004)
<i>Marmota minor</i>	1204	8.30	7.02	
<i>Paenemarmota nevadensis</i>	7644	8.30	7.02	
<i>Pliogale furlongi</i>	946	8.30	7.02	
<i>Prosthennops sp.</i>	135875	8.30	7.02	mass from mean of known estimates in genus
<i>Protohippus sp.</i>	66900	8.30	7.02	mass from mean of known estimates in genus
<i>Pseudaelurus sp. A</i>	22320	8.30	7.02	mass from mean of known estimates in genus
<i>Pseudaelurus sp. B</i>	22320	8.30	7.02	mass from mean of known estimates in genus

Table A.3 continued.

<i>Spermophilus argonautus</i>	131	8.30	7.02	
<i>Sphenophalos nevadanus</i>		8.30	7.02	
<i>Dipoides vallicula</i>	850	7.50	7.00	
<i>Peromyscus pliocenicus</i>	13	7.50	7.00	
<i>Plionictis oregonensis</i>	1030	7.50	7.00	
<i>Pseudaelurus sp.</i>	22320	15.80	7.00	mass from mean of known estimates in genus
<i>Spermophilus sp.</i>	204	10.57	7.00	mass from mean of known estimates in genus
<i>Amebelodon sp.</i>	3810333	7.83	6.90	mass from mean of estimates of <i>A. floridanus</i> in Christiansen (2004)
<i>Antecalomys valensis</i>	13	7.83	6.90	
<i>Copemys esmeraldensis</i>	27	10.57	6.90	
<i>Cupidinimus magnus</i>	23	8.30	6.90	
<i>Dinohippus spectans</i>	536500	8.76	6.90	
<i>Dipoides stirtoni</i>	2589	8.30	6.90	
<i>Diprionomys parvus</i>	11	8.30	6.90	
<i>Goniodontomys disjunctus</i>	58	7.83	6.90	
<i>Hemiauchenia vera</i>	130000	7.50	6.90	
<i>Hesperogaulus wilsoni</i>		7.83	6.90	
<i>Hippotherium sp.</i>	65100	10.57	6.90	mass from mean of known estimates in genus
<i>Hypolagus vetus</i>	483	15.77	6.90	
<i>Hystriocops browni</i>	2500	7.83	6.90	mass from <i>H. venustus</i>
<i>Indarctos oregonensis</i>	2097300	7.50	6.90	
<i>Leptodontomys sp.</i>	6	10.57	6.90	some taxa in genus have mass below 18g; however, there are real m1 length and width measurements for " <i>L. sp.</i> "
<i>Liodontia furlongi</i>	198	8.76	6.90	mass from <i>L. alexandrae</i>
<i>Lutravus halli</i>	5840	8.30	6.90	
<i>Macrognathomys nanus</i>	5	10.57	6.90	
<i>Martes sp.</i>	1767	10.57	6.90	mass from mean of known estimates in genus
<i>Neohipparion leptode</i>	109200	8.30	6.90	
<i>Peromyscus antiquus</i>	31	8.30	6.90	

Table A.3 continued.

<i>Peromyscus sp.</i>	18	7.50	6.90	mass from mean of known estimates in genus
<i>Platygonus oregonensis</i>	98700	7.50	6.90	
<i>Plionarctos sp.</i>	165500	7.50	6.90	mass from <i>P. harlororum</i>
<i>Scalopoides sp.</i>	30	10.57	6.90	mass from mean of known estimates in genus
<i>Simocyon primigenius</i>	33900	7.50	6.90	
<i>Spermophilus gidleyi</i>	700	7.50	6.90	
<i>Tardontia sp.</i>	172	10.57	6.90	mass from mean of known estimates in genus
<i>Castor sp.</i>	14087	7.10	5.90	mass from mean of known estimates in genus; check Silva and Downing (2004)
<i>Dipoides sp.</i>	2669	7.50	5.90	mass from mean of known estimates in genus
<i>Hypolagus oregonensis</i>	501	7.10	5.90	
<i>Machairodus sp.</i>	72300	7.10	5.90	
<i>Mammut sp.</i>	6310400	10.57	5.90	mass from mean of estimates of <i>M. americanum</i> (Christiansen, 2004)
<i>Neotamias malloryi</i>	17	7.10	5.90	
<i>Oregonomys pebblespringsensis</i>	27	7.10	5.90	
<i>Perognathus stevei</i>	11	7.10	5.90	
<i>Plesiogulo marshalli</i>	2820	7.10	5.90	
<i>Pliotaxidea nevadensis</i>	2360	8.30	5.90	
<i>Scapanus proceridens</i>	65	7.83	5.90	
<i>Spermophilus shotwelli</i>	204	7.10	5.90	mass from mean of known estimates in genus
<i>Spermophilus wilsoni</i>	248	7.83	5.90	
<i>Sphenophalos sp.</i>		7.83	5.90	
<i>Teleoceras sp.</i>	883186	9.68	5.90	mass from mean of known estimates in genus
<i>Epicyon saevus</i>	44300	8.30	5.10	
<i>Ammospermophilus hanfordi</i>	58	4.48	4.38	mass from mean of known estimates in genus
<i>Bretzia pseudalces</i>		4.48	4.38	
<i>Dipoides rexroadensis</i>	7095	4.48	4.38	
<i>Eucyon davisi</i>	9000	8.30	4.38	
<i>Megalonyx rohrmanni</i>	3050996	4.48	4.38	mass from mean of known estimates in genus
<i>Megatylopus cochrani</i>	1383500	4.48	4.38	

Table A.3 continued.

<i>Nekrolagus progressus</i>		4.48	4.38	
<i>Ophiomys mcknighti</i>	111	4.48	4.38	
<i>Paenemarmota sawrockensis</i>	5926	4.48	4.38	
<i>Paracryptotis rex</i>	42	4.48	4.38	
<i>Peromyscus nosher</i>	16	4.48	4.38	
<i>Scapanus sp.</i>	97	8.30	4.38	mass from mean of known estimates in genus
<i>Baiomys aquilonius</i>		3.60	3.19	mass from mean of known estimates in genus, but below 18g
<i>Baiomys sp.</i>	8	3.60	3.19	genus mass below 18g; however, there are real m1 length and width measurements for " <i>B. sp.</i> "
<i>Borophagus hilli</i>	52700	4.48	3.19	
<i>Cosomys primus</i>	164	3.60	3.19	
<i>Megalonyx sp.</i>	3050996	7.50	3.19	mass from mean of known estimates in genus
<i>Megantereon hesperus</i>	56900	3.60	3.19	
<i>Mimomys sp.</i>	126	3.60	3.19	mass from mean of known estimates in genus
<i>Neotoma quadriplicata</i>	381	4.48	3.19	
<i>Oregonomys magnus</i>	21	3.60	3.19	
<i>Paenemarmota barbouri</i>	10255	3.60	3.19	
<i>Perognathus maldei</i>	11	3.60	3.19	
<i>Peromyscus hagermanensis</i>	20	3.60	3.19	
<i>Pliogeomys parvus</i>	10	3.60	3.19	
<i>Procastoroides intermedius</i>	12955	3.60	3.19	
<i>Prodipodomys idahoensis</i>	22	3.60	3.19	
<i>Scapanus hagermanensis</i>	97	3.60	3.19	mass from mean of known estimates in genus
<i>Sorex hagermanensis</i>	7	3.60	3.19	
<i>Sorex powersi</i>	8	4.48	3.19	
<i>Sorex rexroadensis</i>	8	3.60	3.19	mass from mean of known estimates in genus
<i>Ursus abstrusus</i>	145500	3.60	3.19	
<i>Alilepus vagus</i>	259	3.60	2.98	
<i>Alilepus wilsoni</i>	146	3.08	2.98	

Table A.3 continued.

<i>Bassariscus casei</i>	832	3.08	2.98	
<i>Borophagus diversidens</i>	75400	3.08	2.98	
<i>Buisnictis breviramis</i>	255	3.60	2.98	
<i>Capromeryx tauntonensis</i>	21600	3.08	2.98	
<i>Dinofelis palaeoonca</i>	87800	3.08	2.98	
<i>Equus simplicidens</i>	204300	4.48	2.98	
<i>Hemiauchenia macrocephala</i>	342900	3.08	2.98	
<i>Hypolagus ringoldensis</i>	319	4.48	2.98	mass from mean of known estimates in genus
<i>Megalonyx leptostomus</i>	2934720	3.08	2.98	
<i>Nekrolagus sp.?</i>		3.08	2.98	
<i>Neotoma fossilis</i>	150	3.08	2.98	
<i>Odocoileus sp.?</i>	101933	3.08	2.98	mass from mean of known estimates in genus
<i>Ophiomys taylori</i>	81	3.60	2.98	
<i>Parailurus sp.</i>		3.08	2.98	
<i>Platygonus sp.</i>	149940	3.08	2.98	mass from mean of known estimates in genus
<i>Plionarctos harroldorum</i>	165500	4.48	2.98	
<i>Procastoroides idahoensis</i>	66745	3.08	2.98	
<i>Procyon sp.?</i>	5353	3.08	2.98	mass from mean of known estimates in genus
<i>Prodipodomys sp.</i>	19	3.08	2.98	mass from mean of known estimates in genus
<i>Puma lacustris</i>	27900	3.08	2.98	
<i>Rangifer sp.?</i>	16900	3.08	2.98	
<i>Sorex meltoni</i>	4	3.60	2.98	
<i>Sorex sp.</i>	8	3.08	2.98	mass from mean of known estimates in genus
<i>Spermophilus howelli</i>	140	3.08	2.98	
<i>Spermophilus russelli?</i>	166	4.48	2.98	
<i>Spilogale sp.</i>	586	3.08	2.98	mass from mean of known estimates in genus
<i>Taxidea sp.</i>	5290	3.60	2.98	mass from <i>T. taxus</i>
<i>Thomomys gidleyi</i>	37	4.48	2.98	
<i>Borophagus sp.</i>	50725	3.60	1.68	mass from mean of known estimates in genus

Table A.3 continued.

<i>Canis lepophagus</i>	17000	3.60	1.68	
<i>Castor californicus</i>	12965	4.48	1.68	
<i>Ceratomeryx prenticei</i>		3.60	1.68	
<i>Cervus sp.?</i>	112483	3.60	1.68	mass from mean of known estimates in genus (Silva and Downing, 2004)
<i>Equus fromanius</i>	172311	1.85	1.68	mass from mean of known estimates in genus
<i>Equus idahoensis</i>	205200	1.85	1.68	
<i>Felis rexroadensis</i>	24500	3.60	1.68	
<i>Ferinestrix vorax</i>		3.60	1.68	
<i>Gigantocamelus spatulus</i>	1669500	1.85	1.68	
<i>Homotherium idahoensis</i>	257900	1.85	1.68	
<i>Homotherium sp.</i>	196425	3.60	1.68	mass from mean of known estimates in genus
<i>Hypolagus edensis</i>	120	3.60	1.68	
<i>Hypolagus furlongi</i>	191	3.60	1.68	
<i>Hypolagus gidleyi</i>	400	3.60	1.68	
<i>Hypolagus voorhiesi</i>	319	3.60	1.68	mass from mean of known estimates in genus
<i>Mictomys vetus</i>	181	3.60	1.68	
<i>Mustela rexroadensis</i>	132	3.60	1.68	
<i>Ondatra idahoensis</i>	698	3.60	1.68	
<i>Ondatra minor</i>	461	3.60	1.68	
<i>Ophiomys meadensis</i>	86	3.60	1.68	
<i>Ophiomys parvus</i>	99	3.60	1.68	
<i>Phenacomys gryci</i>	228	1.85	1.68	mass from mean of known estimates in genus
<i>Platygonus pearcei</i>	149940	4.48	1.68	mass from mean of known estimates in genus
<i>Pliophenacomys osborni</i>	86	3.60	1.68	
<i>Procastoroides sp.</i>	38180	3.60	1.68	mass from mean of known estimates in genus
<i>Satherium piscinarium</i>	18100	3.60	1.68	
<i>Sminthosinis bowleri</i>	1480	3.60	1.68	
<i>Sminthosinis sp.</i>	1480	3.60	1.68	mass from <i>S. bowleri</i>
<i>Sorex palustris</i>	13	1.85	1.68	

Table A.3 continued.

<i>Stegomastodon mirificus</i>	5491333	1.85	1.68	mass from mean of estimates of <i>S. platensis</i> (Christiansen, 2004)
<i>Thomomys</i> sp.	73	3.60	1.68	mass from mean of known estimates in genus
<i>Trigonictis cookii</i>	3130	3.60	1.68	
<i>Trigonictis macrodon</i>	5680	4.48	1.68	
<i>Trigonictis</i> sp.	4587	3.60	1.68	mass from mean of known estimates in genus
<i>Canis edwardii</i>	31100	0.90	0.30	
<i>Hemiauchenia</i> sp.	212040	4.48	0.20	mass from mean of known estimates in genus
<i>Camelops</i> sp.	1409200	3.08	0.10	mass from mean of known estimates in genus
<i>Cervus brevitrabalis?</i>	112483	0.20	0.10	mass from mean of known estimates in genus (Silva and Downing, 2004)
<i>Equus</i> sp.	172311	3.60	0.10	mass from mean of known estimates in genus
<i>Mammut americanum</i>	6310400	4.48	0.10	mass from mean of estimates of <i>M. americanum</i> (Christiansen, 2004)
<i>Panthera onca</i>	97500	0.90	0.10	
<i>Paramylodon harlani</i>		3.60	0.10	
<i>Puma concolor</i>	56700	1.85	0.10	
<i>Taxidea taxus</i>	5290	0.20	0.10	
<i>Lynx canadensis</i>	10900	0.20	0.00	
<i>Lynx rufus</i>	8560	3.08	0.00	
<i>Odocoileus hemionus</i>	96500	0.20	0.00	

Appendix B. Multimodality testing

Testing for multimodality

Histograms are a frequently used method for demonstrating frequency distributions in data. Textbook distributions are typically bell-shaped (symmetric with mean, median, and mode the same) or skewed with one mode (unimodal; Bluman, 2004). However, distributions of data can have more than one mode (U-shaped, bimodal, trimodal, etc.) or no modes at all (uniform; Bluman, 2004). For a more detailed analysis of the modes, a density distribution can be calculated using a kernel density estimate f with a bandwidth h and kernel function K over which the data are analyzed (Silverman, 1981, 1986). I ran this test on log-transformed data using natural logs and bins of size 0 to 1, 1 to 2, etc.

Kernel density estimation

To calculate a kernel density estimate the following equation is used:

$$f(x; h) = \frac{1}{nh} \sum_{i=1}^n K((x - X_i)/h). \quad (\text{B.1})$$

Here, x is the bin size (as equal increments starting at zero to x_i , x_i to x_{i+1} , etc.) and n is the number of samples that fall in each bin; there is no set number of n per bin. X_i is one observation out of n observations to fall in bin x . h is the window width (aka the bandwidth or smoothing parameter) which may overlap bin x and a fraction of the next or h may be just a fraction of bin size x_i to x_{i+1} . h may also overlap multiple bins. The kernel function K may be Gaussian, Epanechnikov, Biweight, Triangular, or Rectangular to

name a few (see illustration of these in Table 3.1 on page 43 in Silverman, 1986). The type of kernel function did not affect the outcome of the test.

Critical window width

As the window width, h , increases it smoothes out the density function by estimating across multiple bins and thus decreasing the resolution of the bin-sampled data. The result of this process is that if a distribution has multiple modes, a larger and larger h will eventually generate unimodal density estimation (Silverman, 1981; 1986). Finding the h that is the transition point at which a density estimation changes from a higher modality to a lower modality (e.g. trimodal to bimodal and bimodal to unimodal) is the critical window width h_{crit} . The method applied in this report is a binary search procedure that calculates the midpoint of a chosen window interval (h_{lo} , h_{hi}) and every subsequent midpoint in the direction of h_{crit} (Silverman, 1981, 1986). I found for the kernel density estimation of the PNW mammalian mass data h_{crit} is approximately 2.3.

Jones' test of h_{crit}

A simulation study in a dissertation by Jones (1983) reveals that 5% of samples drawn from normal distributions with a standard deviation of σ have h_{crit} greater than $h = 1.25\sigma m^{-0.2}$, where m is the total sample size ranging as $40 \leq m \leq 5000$. In this case, with a $\sigma = 3.641$ and $m = 378$, $h = 0.2946$ which is certainly smaller than 2.3 indicating a 95% probability that the Cenozoic PNW mammalian mass data are highly bimodal.

Appendix C: Potential barriers and corridors to migration and gene flow in the late Miocene Pacific Northwest

Isolation for peripatric speciation in the late Miocene Pacific Northwest (LMPN) perhaps required relatively large pre-existing barriers (i.e. topographic highs, large water bodies) positioned jointly with the sudden and massive ash-flow eruptions. However, it cannot be dismissed that some populations perhaps migrated over or through barriers by which they are usually bounded. Below is a description of potential physiographic barriers and corridors to population migrations in the LMPN that surround the source region (Harney Basin) for the widespread eruptions such as the DvCT, PCT, and RST. The information available is made possible by a diverse array of data and analytical techniques from fossil leaf physiognomy to isotopes in fossil tooth enamel to regional syntheses of local structural relationships.

The mountains

In the LMPN, the geographic positions of a number of potential barriers and corridors are similar to ones that exist today. The Western Cascades in Oregon are estimated to be approximately at heights of 800 m based on $\delta^{18}\text{O}$ isotopes in fossil tooth enamel of perissodactyls (i.e. equids and rhinocerotids; Kohn et al., 2002; Kohn and Dettman, 2007; Kohn and Fremd, 2007). Evidence in the rock record providing estimates of total thicknesses of deposits in this range is difficult to evaluate since today vegetation covers much of what would be exposed (du Bray et al., 2006). The bulk of the deposits are seen in the Sardine (Thayer, 1937) and Troutdale (Beeson and Tolan, 1987)

Formations with the majority of the Sardine eruptions and Troutdale fluvial deposits occurring between 13 and 9 Ma (Orr et al., 1999) and 12 and 6 Ma (Beeson and Tolan, 1987), respectively. Though perhaps not as high as the present-day High Cascades, the Western Cascades would have covered a wider area with the earliest eruptions to the west (42 Ma) and youngest to the east (10 Ma). This eastward trend of eruptions is attributed to clockwise rotation and the then shallowing of the subducting Farallon Plate (Orr et al., 1999). The volcanic activity only temporally overlaps with the eruption of the DvCT, while the Troutdale fluvial deposits are contemporaneous with all three ash-flows (DvCT, PCT, and RST). Additionally, Reiners et al. (2002) indicate the Washington Cascades were being uplifted at a rate of 0.5-1 km/m.y. from 12 to 8 Ma. The LMPN Western Cascades extended from approximately 48° N latitude in northwestern Washington (duBray et al., 2006) to perhaps as far south as the Tahoe-Reno area in California (Cousens et al., 2008).

The Klamath Mountains were much higher in the LMPN than they are today. Based on estimates of Mortimer and Coleman (1985), an approximately 70,000 km² dome centered on Condrey Mountain just south of the California-Oregon border may have raised this area of the Klamath Mountains up to a maximum of 7000 m from 14 to 5 Ma. Today, the elevation of Condrey Mountain is 2168 m. Causes for the doming are unclear at present, but may be due to eastward compression (Mortimer and Coleman, 1985).

In the Basin and Range, Wolfe et al. (1997) indicate that range heights were similar to today. These estimates are based on approximations of enthalpy related to

measurements of fossil leaf characteristics (e.g. leaf margin, size, apical and basal configurations, length to width ratios, and general foliar shape as just six parameters of the 29 evaluated by this method). The Basin and Range today extends into Oregon south of Harney Basin as expressed in Steens Mountain and Hart Mountain. Steens Mountain was perhaps uplifted in the late Miocene. Evidence for this lies in two parts: 1) the DvCT (9.7 Ma) is observed on the eastside of Steens Mountain while the PCT and RST are only observed to the west of the uplifted block (Streck and Ferns, 2004). Despite this, Singleton and Oldow (2004) indicate deformation of the Alvord-Steens fault system initiated after 7 Ma based on volcanoclastic sediments being cross-cut by the fault system. 2) At approximately 10 Ma is when the first eruptions at the north end of Steens Mountain begin in the Brothers Fault Zone and continue to erupt further away to the northwest as time passes (Camp and Ross, 2004). This potentially indicates structural stress related to clockwise rotation (Orr et al., 1999) or an expanding plume head (Camp and Ross, 2004). Perhaps in this time (10-7 Ma) Steens Mountain attained comparable elevations as today or already was an area of considerable topographic relief after the DvCT erupted. It is unclear if the Brothers Fault Zone and the Alvord-Steens fault system are related (Pezzopane and Weldon, 1993).

Southeast of Steens Mountain the track of the Yellowstone Hotspot had developed the McDermitt (16.5-15 Ma), Owyhee-Humbolt (14-12 Ma), and Bruneau-Jarbridge (12.5-11 Ma) volcanic fields and was in the process of developing the Twin Falls (12-6.5 Ma) and Picabo (10.5-6.5 Ma) volcanic fields (Beranek et al., 2006). These volcanic fields may have attained elevations of 1000 m and stood as a continental divide

(Pierce and Morgan, 1992; Beranek et al., 2006) much like at Yellowstone National Park today. Moreover, Beranek et al. (2006) found isotopic evidence from detrital zircons in regional sediments suggesting that the McDermitt, Owyhee-Humbolt, and Bruneau-Jarbridge volcanic fields acted together as a northeast trending drainage divide. In addition to the elevated volcanic fields, the Atlanta lobe of the Idaho Batholith was uplifted and contemporary with the hotspot bulge of the Twin Falls and Picabo volcanic fields (Beranek et al., 2006). Together these features were likely a topographic high from northern Idaho and western Montana down to northeastern Nevada by 9 Ma.

West of the Atlanta lobe the elevation of the Wallowa Mountains was 2000 m by 10 Ma according to Hales et al. (2005). This uplift followed a potential brief subsidence and was simultaneous with initial eruptions of Columbia River basalt. Uplift is suggested by Hales et al. (2005) to be produced by convective upwelling and detachment of a plutonic root which arrived at isostatic equilibrium by 12 Ma.

Blue Mountain uplift is considered to have begun in the early Oligocene (~30 Ma). Robinson et al. (1990) observe that the eastern sub-region (cf Robinson et al.'s [1990] "facies") of the John Day Formation pinches out northeast of the town of Kinzua where middle Miocene Picture Gorge Basalt overlies the Eocene-Oligocene Clarno Formation. The Picture Gorge ash-flow tuff of the John Day Formation (28.7 Ma; aka Picture Gorge ignimbrite [PGI] of Fisher and Rensberger, 1972) is not found in the western sub-region of the John Day Formation. The phenomenon is the same for ash-flow tuffs in the western subregion where sediments also pinch out against a "Clarno high" (Robinson et al., 1990). Only ash fall tuffs (e.g. Deep Creek tuff) can be found in both

western and eastern subregions of the John Day Formation (Robinson et al., 1990). Interestingly, in the Paulina Basin (southern sub-region), the PGI is apparently very distal (T. Fremd, pers. comm., 2007). This might indicate that the Ochoco Mountains were uplifted subsequently to 28.7 Ma. It may be that later structural deformation of the area continued into the earliest Miocene. The Kimberly Member in the eastern sub-region of the John Day Formation is capped in some localities by erosional unconformity followed by Picture Gorge Basalt representing a hiatus of eight million years (Hunt and Stepleton, 2004). However, by the time of the eruption of the Harney Basin tuffs the region may have produced the bulk of its deformation as indicated by 1) few faults cross-cutting the overlying Deschutes Formation (10-8 Ma; this is confusing however, because Smith (1985) has constrained the age of the Deschutes Formation as ~7.6-4 Ma from the dated Pelton Basalt and Round Butte Basalt, respectively) west of the Blue Mountains (Farooqui et al., 1981; Robinson et al., 1990) and 2) Streck and Grunder (1995) observing Aldrich Mountain as a potential “hurdle” for the RST to pass over. However, uplift may not be uniform throughout the region as indicated by fanglomerates in the Rattlesnake Formation (~7.5-7.05 Ma; Retallack et al., 2002) in western John Day Valley.

The Strawberry Mountains were present in the LMPN. However, their activity had largely ceased by 10 Ma (Walker, 1990). By this time of eruptive cessation, the Strawberry Mountains had built up 2000 m of a diverse array of volcanic deposits over 3400 km² near the eastern end of the John Day Valley (Walker, 1990).

The rivers

Prior to the Pliocene the ancestral Columbia River flowed north of its present border position at north-central Oregon and south-central Washington (Fecht et al., 1987). Following the emplacement of the Priest Rapids Member (14.5 Ma) of the Wanapum Basalt Formation (Columbia River Basalt Group [CRBG]), the ancestral Columbia River established the Bridal Veil channel that traversed from approximately 20 to 30 km north of its position at The Dalles, Oregon to approximately line up with the modern channel's course at Hood River, Oregon. The Bridal Veil channel lasted through the late Miocene into the early Pliocene (Beeson and Tolan, 1987). Compressional folding and rapid uplift of the High Cascades region has since made the river antecedent in its present location through the Columbia River Gorge (perhaps since ~2 Ma; Beeson and Tolan, 1987). Further east, Fecht et al. (1987) indicate in the late Miocene to middle Pliocene the ancestral Clearwater-Salmon River captured the ancestral Yakima-Columbia River channel in the subsiding Pasco Basin of the central Columbia Plateau following the deposition of the Ice Harbor Member (8.5 Ma) of the Saddle Mountains Basalt. The Ice Harbor Member underlies the Ringold Formation (8.5 – 3.4 Ma; Fecht et al., 1987) in Pasco Basin. However, it appears in Figures 11 and 12 of Fecht et al.'s (1987) report that the Lower Monumental Member (6 Ma) of the Saddle Mountains Basalt is deposited prior to this river capture event. No middle to late Miocene confluence further west between these two ancestral streams has been proposed by either report. It appears there is some likelihood the ancestral Clearwater-Salmon River flowed west south of the ancestral Yakima-Columbia River in the late Miocene. Perhaps this confluence took place north of present-day Mt. Hood.

The ancestral John Day River was sourced by continued uplift of the Blue Mountains and surrounding region in the late Miocene. Retallack et al. (2002) indicate Picture Gorge Basalt, Mascall and John Day Formation sediments, and ash falls from the east and south of the region were the materials that were deposited to form Rattlesnake Formation paleosols in the western John Day Valley. Moreover, clast imbrication measurements indicate the paleodrainage flowed southeast down the axis of the valley (as illustrated by isopachs of the RST (Streck and Grunder, 1995)) prior to being choked with thicker and coarser alluvial fan material with channels flowing south (Retallack et al., 2002). Perhaps this indicates that the John Day River flowed southeast to Lake Idaho (~9.5-2.5 Ma; Beranek et al., 2006) in the western Snake River Plain or somehow was associated with some ancestral river coarse to the north (ancestral Clearwater-Salmon River?). Today the John Day River flows northeast in the John Day Valley before its incision through Picture Gorge Basalt and the John Day Formation finally joins with the Columbia River.

The ancestral Deschutes River as indicated from paleocurrent measurements in sediments below “valley” filling basalt flows of the Pelton Basalt (~7.6 Ma; Smith and Snee, 1984) indicate a northward flow (Smith, 1985). Smith (1985) further describes evidence for only a single main stream in the southern Deschutes River Valley as opposed to two (Deschutes and Crooked Rivers) today.

The ancestral Snake River is more of a mystery than other major rivers in the Pacific Northwest. Wheeler and Cook (1954) indicate that the direction of the Snake River today would not have been established until approximately 2.5 Ma by forging an

outlet for Lake Idaho through the uplifted Wallowa Mountains. The ancestral Snake River is suggested to have flowed either through southeastern Oregon (Wheeler and Cook, 1954; Minckley et al., 1986) or through northern Utah and Nevada (Minckley et al., 1986; Repenning et al., 1995; Link et al., 2002; Hershler and Liu, 2004). To date, no clear geological evidence supports these proposals while it is known that multiple rivers such as the ancestral Owyhee River flowing north through the Oregon Idaho graben (Cummings et al., 2000) and streams of the eastern Snake River Plain (Beranek et al., 2006) flowed into the internal drainage system of Lake Idaho. However, in a summary by Carney and Page (1990), it appears there are potential linkages of the Klamath Basin (Oregon) and Mohave Basin (southern Great Basin) to the ancestral Snake River established on the basis of paleoichtheological relationships between the fossil Teleost fish *Ptychocheilus arciferus* of the Glens Ferry Formation (5 – 3 Ma) in Idaho and its descendent relatives, *P. oregonensis*—of present-day Oregon, Washington, and Idaho—and *P. grandis* in the Sacramento Basin in California.

The basins

Multiple basins, such as the Deschutes, Tygh Valley, Dalles, Arlington, Agency, Walla Walla, John Day, Paulina, Harney, Juntura, Harper, and Boise basins were present 10 to seven Ma (Walker, 1990). Most of these basins are constrained by age-dated basalt flows and tuffs and/or with paleontological evidence. Harney Basin itself is considered to have been subsiding gradually with the release of the three major ash-flow tuffs, DvCT, PCT, and RST (Walker, 1979). Northeast of present-day Steens Mountain subsidence of

the Oregon-Idaho graben was complete (15.5-10.5 Ma; Cummings et al., 2000), while subsidence of the western Snake River Plain had begun thereafter (~11 Ma; Beranek et al., 2006).

Regarding the central region of Oregon, measured thicknesses of the DvCT (<35 m; Greene, 1973) and RST (<70 m; Streck and Grunder, 1995) indicate low relief topography throughout most areas as indicated by uniform thicknesses. Where the RST is at its thickest, it is thicker than where the DvCT is at its thickest. Some regions with RST, such as the John Day Valley and south of Harney Basin, might have been areas of much lower elevation as the thicknesses are greater there than in their respective surrounding landscapes (Streck and Grunder, 1995).

Appendix D. FVC-Albedo data table

Table D. 14 observations of *FVC* (%) and Albedo (%) for different biomes throughout the world.

Biome	<i>FVC</i> (%)	Albedo (%)	Albedo Source
forest/woodland	0.924*	0.24	Fuller and Ottke, 2002
forest/woodland	0.924*	0.125*	Barry and Chorely, 1992
forest/woodland	0.924*	0.1065*	Betts and Ball, 1997
grass/sav	0.755*	0.31	Fuller and Ottke, 2002
grass/sav	0.755*	0.476*	Betts and Ball, 1997
woody grass/sav	0.88	0.25	Fuller and Ottke, 2002
woody grass/sav	0.88	0.215*	Barry and Chorely, 1992
woody grass/sav	0.88	0.180*	Betts and Ball, 1997
crop	0.87	0.23	Fuller and Ottke, 2002
crop	0.87	0.215*	Barry and Chorely, 1992
urban	0.79	0.24	Fuller and Ottke, 2002
closed shrub	0.76	0.33	Fuller and Ottke, 2002
open shrub	0.42	0.45	Fuller and Ottke, 2002
barren	0.14	0.53	Fuller and Ottke, 2002

FVC data from Zeng et al., 2003.

* Averaged from given range

Appendix E. AE-MAP regression data table

Table E. 15 observations of AE , $MAP_{\min}$, $MAP_{\max}$, and MAP_{mean} for different locations throughout the world. AE data from Rosenzweig (1968). AE and MAP_{mean} were regressed with a zero intercept as $AE = 0.6719 MAP_{\text{mean}}$

AE	$MAP_{\min}$	$MAP_{\max}$	MAP_{mean}	Location	MAP reference
126	127	254	191	Nye Co. NV	nationalatlas.gov
200	200	410	305	Cape Thompson, AK	Worldbook.com
617	762	889	826	Norman, OK	nationalatlas.gov
562	750	1000	875	Toronto, ON	statcan.gc.ca
1230	1250	2500	1875	Kade, Ghana	bestcontryreports.com
1318	1241	2432	1709	Yangambi, D.R. Congo	Wilkie et al., 1999
219	254	381	318	Rexburg, ID	nationalatlas.gov
832	1270	1524	1397	Oak Ridge, TN	nationalatlas.gov
178	127	254	191	Hanford Res., WA	nationalatlas.gov
1000	-	-	1500	Darwin, AUS	bom.gov.au; ypri.vic.gov.au
650	900	1200	1050	Sydney, AUS	bom.gov.au; ypri.vic.gov.au
350	300	600	450	Port Headland, AUS	bom.gov.au; ypri.vic.gov.au
528	-	-	745	El Destierro I (550 m), Argentina	Perez and Frangi, 2000
503	-	-	786	El Destierro I (850 m), Argentina	Perez and Frangi, 2000
465	-	-	828	El Destierro I (1025 m), Argentina	Perez and Frangi, 2000