

ANTHROPOGENIC COMMUNITY DISTURBANCE: GENERAL PATTERNS,  
QUALIFICATIONS, AND ANIMAL-MEDIATED NUTRIENT TRANSPORT

By

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To 私の婚約者山口すみれの君

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## LIST OF ABBREVIATIONS

CI	Confidence Interval
CV	Coefficient of Variation
K	Potassium
N	Nitrogen
P	Phosphorus
PCL	Peirce's Criterion Limit
ppt	Parts per thousand
RI	Ruggedness Index
ROC	Receiver Operating Characteristic
LSNWR	Lower Suwannee National Wildlife Refuge
TKN	Total Kjeldahl Nitrogen

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Ecology has tended to ignore or avoid human impacts for many reasons; yet they are pervasive and must be incorporated into general ecology. Broad patterns of anthropogenic community modification (decreases in maximum body size and home range of consumers; increases in community change rate, novel resources, and relative importance of generalists; and shifts in the importance of top-down vs. bottom-up control) should generate predictable changes in animal-mediated nutrient transport, such as: altered importance, shortened distances, increased cross-habitat transfers, and increased flow into refuges. A case study of an exotic generalist, Feral Hogs (*Sus scrofa*), is used to examine these expected changes and their landscape dependencies. Hogs affected herbaceous species richness and percent cover, but not biomass, in landscape-specific ways reflecting the juxtaposition of refuge and feeding habitats. The hogs influenced nutrient flows in the system. The source of the nutrients deposited on the islands was the marsh: both fecal and stable isotope analysis revealed a diet largely of the marsh plant American Bulrush (*Schoenoplectus americanus*). Based on dietary and phenotypic differences between coastal and inland hogs, transport distances were short. Thus the role the hogs play in the system are consistent with the hypothesized

effects that generalists have on nutrient transport in human-impacted systems: short-distance inter-habitat flow into refuge areas from resource areas. The patterns of human impacts hypothesized here and examined with the case study of Feral Hogs in Florida coastal ecosystems are placed in a broader context by examining cultural perceptions of wilderness. A basal definition of wilderness is presented that can act as a starting point when attempting to understand differing wilderness concepts among cultures. Land use patterns should differ among cultures in ways that reflect concepts of wilderness. Wilderness archetypes were established from Germany (forests) and Korea (mountains). Land use patterns were found to differ with wilderness archetype. These results indicate the important, but largely unrecognized, influence cultural details have on land use patterns and thus anthropogenic disturbance of biotic communities.

## CHAPTER 1 OVERVIEW

The science of ecology has largely focused on natural systems with presumed minimal human disturbance (Collins et al. 2000). However, anthropogenic impacts have a long history of ecological study: indeed one of the earliest published ecological observations was by the Greek philosopher Plato in c. 360 BCE, who in a dialogue describing the history of the peninsula of Attica (where Athens is located) has Critias state:

In its great fertility our land far surpassed any other, for it was then capable of supporting a great army of men who did not work the land. [...] What has now survived of this land can rival any other land in the variety and quality of its crops and the pasture it offers all species of animals. But, at that time, our land produced all this not only of high quality but in great abundance. You might ask how this is credible and how our present land could possibly be called a vestige of our earlier land.

[...] Many and great were the floods [...] and during this succession of natural disasters the soil was washed down from the high places. It did not form any considerable alluvial deposits, as in other regions, but it disappeared into the deep, as in flood after flood it was continuously washed into the sea from all sides. What actually remains is like our small and barren islands, and, compared to the land it once was, Attica of today is like the skeleton revealed by a wasting disease, once all the rich topsoil has been eroded and only the thin body of the land remains. But in that age our land was undiminished and had high hills with soil upon them; what we now call the Rocky Barrens were covered with deep rich soil. And in the mountains there were dense forests of which there still survives clear evidence. Some of our mountains can now grow just barely enough for bees, but it was not so long ago that [lofty trees grew there]. There can still be found intact rafters cut from trees that were felled and brought down to be used for the greatest building projects. And there were many trees that were cultivated for their fruit and they provided limitless fodder for flocks of sheep and goats.

Every year there was a harvest of Zeus-sent rain. It was not lost, as it is now, as it flows off the hard surface of the ground into the sea, but the deep soil absorbed the rain and it stored it away as it created a reservoir with a covering of clay soil above it; and, as it distributed the water it had absorbed from the high places into its hollows, it produced an abundant flow of water to feed springs and rivers throughout every region of the country.

[...] The land was cultivated with great skill [...] by farmers [...] who [...] possessed a most fertile land and water in abundance, and above this land a climate and seasons that were most temperate.

[...] [T]he acropolis was very different then than it is now. A single night of torrential rain stripped the acropolis of its soil and reduced it to bare limestone in a storm that was accompanied by earthquakes. Before the destructive flood of Deucalion, this was the third such cataclysmic storm [...] It was entirely covered by soil and, except for some small outcroppings, level on the top. [...]

There was a single spring in the location of the present acropolis, but it has been choked by the debris of earthquakes [of that night], and its waters now flow only in a trickle [...] But it provided men of that age with an abundant supply of water.

(Clay 1997, pp. 1296-1298)

Plato was clearly aware of the devastating ecological changes that had occurred in Greece due to human activities and, intriguingly, he made the connections between loss of vegetative cover, soil erosion, increased rain runoff, and lowered water tables.

However, he attributed these changes to cataclysmic natural events—great floods and earthquakes—rather than chronic mundane human activities such as cutting timber, fire, and livestock grazing (Hughes & Thirgood 1982). But the themes Plato identified still resonate as environmental concerns today.

More recently, the study of ecology in a particularly anthropogenic habitat—abandoned agricultural fields, leading to what is called old field succession—has been a font of ecological theories of competition, facilitation, and community assembly (Billings 1938; Clements 1916; De Steven 1991; Inouye et al. 1987; Odum 1960; Oosting 1942; Oosting & Humphreys 1940). Also, there has been a recent increase in interest in studying ecological patterns and processes in specifically anthropogenic landscapes and habitats (such as urban ecology) (McDonnell & Pickett 1993; Pickett et al. 2001; Wetterer 1999), and a newly minted NSF center (U. of Maryland) is focused on the

interface between human and natural processes. However, the realizations that rather few ecosystems were functioning in a completely pristine state even at the time of first scientific observation and that essentially no ecosystems are operating free of human influence under the present regime of anthropogenic climate change, nitrogen deposition, and other impacts are being but slowly incorporated into ecological paradigms and study designs (Barlow et al. in press; Ellis & Ramankutty 2008; Vitousek 1994; Vitousek et al. 1997b).

There are many reasons why anthropogenic influences might be ignored by ecologists. Rational reasons, including the desire to study a system in equilibrium or with a complete species complement and patterns of landscape and food web connectivity, the minimization of noise in the data, establishment of a baseline, *etc.*, are numerous and valid (Noss & Cooperrider 1994; Papworth et al. 2009). An untouched pristine system is likely to be closer to some kind of long-term equilibrium relative to a system subjected to continually shifting anthropogenic pressures. Therefore, population demographics, interspecific interactions, food web characteristics, ecosystem feedbacks, and other measurable qualities are more likely to have reached potential equilibrium states (be they dynamic or stable point attractor). In contrast, a system with anthropogenic influences might be undergoing relatively fast changes, in effect existing in an unbalanced transient state that would make interpretation and generalization of the data difficult. For example, predator:prey ratios likely differ tremendously between natural systems and anthropogenic systems in which the predators are artificially maintained at high levels due to human supplementation of their diets, as occurs with

mesopredators in suburban and urban settings (Robinson & Wilcove 1994). This could set prey into long-term trajectories towards extinction.

Pristine ecosystems gain and lose species fairly slowly compared to systems under anthropogenic influence, particularly because dispersal is usually constrained to quite local scales. It is reasonable to assume that when one observes a community in a natural state complements of species and functional groups present are essentially complete and operating largely in the evolutionary contexts to which their traits are adapted. Studying species relationships and adaptations is much more difficult when important species been extirpated from a system or behaviors are maladaptive under the anthropogenic regime. The traits of species still present in effect are adapted to a community context that no longer exists. For example, the fragmentation of the eastern forests of North America has resulted in an increase in Brown-headed Cowbirds, an important nest parasite on song birds that prefers open areas and therefore most strongly impacts forest birds near the edge of the forest (Robinson & Wilcove 1994). Under these new conditions of fragmentation, augmented by food supplementation in agricultural systems that can sustain high cowbird abundances, the acceptance of cowbird eggs by the host parents is a doomed strategy. Yet some host species seem to show no discrimination. This maladaptive behavior seems difficult to understand, until one recalls that under past conditions there was little danger of parasitism by the majority of forest song birds and therefore no need for egg discrimination. So the current host behaviors are maladaptive in the recently changed, current environment.

The establishment of baseline ecological data, when possible in systems that have not been greatly perturbed by humans, is of course extremely important to be able to

understand how systems change and respond to perturbations. Tracking anthropogenic impacts today is of fundamental importance and assessing these impacts require baseline data, either temporal, to track how a particular system changes through time, or spatial, to determine how one system is being affected by comparing it to a similar system with less anthropogenic influence.

In addition to the plethora of rational reasons to study systems with little anthropogenic presence, it is likely that emotional reasons also play large roles. In spite of the much purported objectivity of scientists, it is no secret that ecologists tend to share an emotional (and some might go so far as to say spiritual) bond with Nature (Wilson 1984). This may lead to a kind of bias in the foci of ecological studies: anthropogenic impacts, which tend to be destructive and unsightly, are distressing to dwell on, and so may be much less studied. Moreover, anthropogenic landscapes almost by definition have humans present, and their imprints, which means that humans must be included among the objects of study. Anthropology is the study of humankind. Yet there has traditionally been a gap between ecology and anthropology in terms of study subjects and frames of reference that likely implicitly reflects the importance of the Great Divide (the Human/Nature dichotomy) in human perceptions of reality (Callicott 2007; Oelschlaeger 2007).

As human populations and resource use burgeons, it is becoming increasingly both more important to study anthropogenic impacts and more difficult to find systems that are uninfluenced by humans—human impacts in effect are becoming pervasive across the globe.

This study is an attempt to address this issue, including conceptual reviews, a detailed case study, and analyses of cultural perceptions of wilderness. One issue is assessing overall patterns of biotic community change over the entire gradient of anthropogenic influence. There is increasing attention being given to the interplay of population and community processes and ecosystem processes such as nutrient pools and dynamics (the meta-ecosystem process; Leibold et al. 2010; Loreau et al. 2003). Therefore, one theme that is a particular focus of this dissertation is anthropogenic changes in animal-mediated nutrient flows. To this end, in Chapter 2 a series of conceptual models of community traits that are vulnerable to anthropogenic influence are explored and discussed. Although mainly focusing on vertebrates, some of the conceptual models presented there involve community traits that directly involve or touch on other taxa as well. The emphasis on vertebrates derives from my focus on the influences anthropogenic impacts have on animal-mediated nutrient flows, which are likely to be particularly mediated by vertebrates. This issue is explored conceptually in this chapter, especially the increased role of generalist omnivores in anthropogenic landscapes. Hypotheses are developed as to the types of changes likely to be seen in animal-mediated nutrient flow along the gradient of human influence.

In Chapters 3 and 4, these hypotheses are examined in a case study exemplifying the type of generalist omnivore likely to be becoming dominant in animal-mediated nutrient flows in human-dominated landscapes. This case study involves Feral Hogs (*Sus scrofa*) and their impacts in Florida coastal ecosystems. Feral Hogs are an exotic species of global concern (Oliver & Brisbin 1993). From domestication centers in Eurasia, they were taken and subsequently released or escaped from captivity

throughout the world, becoming pests first in Melanesia and throughout the Pacific islands and later in Australia, New Zealand, North and South America, and more oceanic islands (Oliver & Brisbin 1993).

Because of their feeding strategy of rooting and breeding potential, Feral Hogs have often proved devastating to native ecosystems (Hone 2002; Nogueira-Filho et al. 2009; Vitousek et al. 1997a). As generalists, they successfully colonize ecosystems as diverse as scrub deserts to tropical rainforests (Saunders & McLeod 1999). Not only are they themselves a major component in human impacts on many ecosystems, but they also represent the type of generalist (whether exotic or native) that is expected to increase in communities under human influence.

Chapter 3 examines how Feral Hogs influence local plant communities. Feral Hog impacts on characteristics of the herbaceous community of the coastal hammock system on the gulf coast of Florida are examined, specifically species richness, cover, and biomass. The impacts of the hogs were experimentally examined through the use of hog exclosures and artificially tilled plots (mimicking rooting) compared to paired control plots.

The presence of the coastal hammock both lining the coast and as islands dotting the tidal marsh enabled an examination of the importance of landscape patterns of resource juxtaposition (marsh feeding areas and hammock resting areas) because treatment effects could be compared between the islands and the mainland.

In Chapter 4, the hypotheses introduced in Chapter 2 regarding the nutrient transport syndrome of generalists in a human-influenced area are examined in detail for the case study of the Feral Hogs. The source of the nutrients transported by the hogs is

established through fecal dietary analysis and stable isotope analysis of bone tissues and foods. The destination of the transported nutrients is determined through fecal surveys (an index of nutrient inputs), and the importance of the nutrients to the herbaceous community is examined through nutrient analyses of the soil and herbaceous biomass. As in Chapter 3, the influence of landscape patterns and habitat juxtaposition is addressed. The potential for long-distance nutrient transport by Feral Hogs is gauged through stable isotope analysis of hogs at different distances from the coast and through studies of genetic population structure, both with opportunistically gathered data on hog phenotypes and with a more formal genetic analysis using microsatellites gleaned from fecal samples.

The case study contained within Chapters 3 and 4 illustrates in a concrete fashion many of the concepts introduced in Chapter 2. This case study shows that impacts of introduced vertebrates on community composition and nutrient flows can be profound and apply even to a largely natural system on the lower half of the gradient of anthropogenic influence proposed in Chapter 2.

However, human impacts differ by more than just the position on an anthropogenic gradient. The latter section of this study recognizes the need to sometimes qualify the generalizations that can be made about anthropomorphic changes with cultural details that influence the way people interact with their environment. As cultural views on the position of humans in relation to the natural world are likely important in determining how people will choose to use a landscape, Chapter 5 delves into the Great Divide and addresses the differences and core similarities of differing cultural definitions of wilderness. Problems arising from differences among these definitions are especially

germane to conservation efforts, which often incorporate people, strategies, and science from multiple nations and thus lead to a lack of understanding across cultural divisions. It is hoped that some of these problems can be more easily understood and overcome with an acknowledgement of the universality in human cultures of a basal wilderness concept upon which the diversity of perspectives is built.

Chapter 6 takes this basal wilderness concept one step further. Using a comparison between current cultures (mostly Korea and Germany), I examine how differing wilderness archetypes can lead to divergent land use patterns. Wilderness archetypes are examined in traditional folktales as well as in the names of current protected areas. These two sources are likely to reflect the ideals of the peoples rather than just the realities of their environments. The land use patterns are examined in light of the distinction between cultural areas and wilderness made within particular cultures. The influence of wilderness archetypes (and whether they are based on topography or land cover) on land use decision rules is examined by comparing the ruggedness of cultural areas and wilderness areas between different cultures and with elevational transects perpendicular to the cultural-wilderness borders. Differences in the resistance of a wilderness archetype to development is likely to alter conservation issues and priorities and thus different nations will have unique challenges that will be difficult to understand without an examination of the cultural perspective.

Thus, this work is a multifaceted attempt to integrate broad trends in human ecology with animal-mediated nutrient transport and landscape patterns of habitat juxtaposition, while recognizing the influences of differing cultural norms on the development of landscape patterns and fragmentation. It is broad and ambitious in

scope, with the hopes of synthesizing information from divergent fields to provide a better perspective on the issues surrounding human interactions with their world.

## CHAPTER 2 CHANGES IN NUTRIENT TRANSPORT PROCESSES OVER GRADIENTS OF ANTHROPOGENIC COMMUNITY MODIFICATION

### **Introduction**

Before being driven extinct by human actions in the early 20<sup>th</sup> century, the Passenger Pigeon (*Ectopistes migratorius*) was the most numerous bird in the world, forming enormous migrating flocks of hundreds of millions that periodically blackened the skies across most of eastern North America. Early observers noted that the depth of the pigeon guano under roosting sites was typically several centimeters thick, sometimes reaching over 50 cm deep. This amounted to an estimated deposition of 8 kg of nitrogen (N) and 1 kg each of phosphorus (P) and potassium (K) per hectare in nesting areas over the 30 day breeding cycle. The much denser roosting sites would have received an estimated 45 kg N and 7 kg each of K and P per hectare in a single night (Ellsworth & McComb 2003), concentrating nutrients gleaned from a much larger feeding area. Because the area impacted annually by nesting was likely ~10 million hectares and by roosting was likely ~5 million hectares, the extinction of the Passenger Pigeon must have caused massive but undescribed changes in ecosystem nutrient cycles, flows, and budgets across eastern North America (Ellsworth & McComb 2003).

The extinction of the Passenger Pigeon ended the concentration of nutrients derived from foraging areas of 20,000 to 80,000 km<sup>2</sup> into roosting areas that were only 0.02 to 10 km<sup>2</sup> and nesting areas that were typically 80 km<sup>2</sup> by 3 – 5 billion birds over the eastern portion of North America. The devastation to woody vegetation caused by the shear biomass of roosting birds and the elimination of undergrowth by guano deposition is well documented, but the impacts of the elimination of pigeon-mediated

nutrient transport and concentration on the eastern forests are unknown (Ellsworth & McComb 2003).

Other examples of the importance of animal-mediated nutrient transport include the introduction of foxes to previously predator-free islands in the Aleutian archipelago that reduced nesting seabird populations and the marine-derived nutrients they transported to such an extent that the plant community shifted from nutrient-rich grasslands to tundra (Croll et al. 2005).

Sea turtle nesting introduces a significant amount of nutrients into the beach dune systems. Along a 21 km stretch of beach, 14,305 loggerhead turtle nests deposited over 1000 kg of nitrogen and 93 kg of phosphorus, leaving over 700 kg N and 57 kg P in the system after the successful hatchlings returned to the ocean. Because sand is so nutrient poor, this input is likely extremely important for the plant growth that stabilizes coastal dunes around the world and has likely been significantly reduced by anthropogenic reduction in global sea turtle numbers (Bouchard & Bjorndal 2000).

While Mohr et al. (2005) found that the exclusion of Wild Boar and Red Deer and thus their nutrient donations reduced soil fertility in a European forest, the impacts of animals on the nutrient budgets of an ecosystem are often much more complex than simply moving things around. As found in the wildebeest migration system of the Serengeti, the nutrient transport of large migrating herds of ungulates can be overshadowed by their indirect effects such as increasing the speed of nutrient cycling (through digestion of plant matter) and reducing the frequency of fire (through reduction in fuel loads), a significant route of nitrogen loss in many systems (Holdo et al. 2007).

In spite of the fact that patterns of nutrient and energy flow within ecosystems have long been central to ecology and understanding the functioning of ecosystems (Evans 1956), it is only recently that the importance of animal mediated nutrient flows between different ecosystems, such as the examples above, has become recognized (Polis et al. 1997; Vanni & Headworth 2004). This recognition rests on two pillars of ecology: nutrient/energy flow and the distributions and abundances of species. Nutrient flows between ecosystems can be disrupted by population reductions and extinctions of some nutrient transporters (Sekercioglu 2006) or by the increase in importance of others, including exotic species (Ehrenfeld 2010). Many of these population changes leading to altered nutrient fluxes are caused or exacerbated by anthropogenic community changes, habitat reduction, degradation, or fragmentation. In turn, changes in patterns of nutrient flow can alter competitive interactions within communities (Keddy et al. 2000), vulnerability to exotics (Thompson & Leishman 2005), and even the physical structure of communities (Croll et al. 2005), likely leading to further community and nutrient flow changes.

It is therefore necessary to understand how human activities in general tend to affect biotic communities and how those changes translate into changes in nutrient flow patterns across landscapes to fully understand how ecosystems respond to anthropogenic influences.

### **Predictable Human Impacts**

In spite of the wide range of human cultures, technologies, and subsistence systems, there appear to be predictable progressions of community alteration along the gradient of degree of human influence. While the gradient is multi-dimensional and involves many direct and indirect anthropogenic impacts, it is strongly associated with

population density (Ellis & Ramankutty 2008). The gradient may be temporal, spatial, or both. A previously untrammelled region may be subjected to greater levels of use and settlement, with anthropogenic impacts increasing through time. Alternatively, a system with stable anthropogenic presence can have spatial gradients from rarely exploited hinterlands (or protected areas) to urban areas. Of course, anthropogenic presence is unlikely to be stable so a combination of both spatial and temporal gradients is probably most common as anthropogenic impacts wax and wane with population densities, use intensities, and the rise and fall of civilizations.

Here I unite the historical and spatial perspectives of anthropogenic change as two expressions of the same process. My goal is to present a synthesis of many ideas and perspectives that are familiar in conservation biology and ecology but to my knowledge have not been integrated together with nutrient transfer processes before. Along the gradient of increasing anthropogenic impact, there appears to be a relatively predictable progression of general community changes (Figure 2-1). (Although specific ecosystem or cultural characteristics in some cases can lead to unpredictable types of changes such as potential alternative stable states or differing land use patterns (Worman 2010), these can be considered as overlays and refinements to the general pattern.)

I focus on six general ecosystem qualities that are likely to be particularly germane to anthropogenic alterations of animal-mediated nutrient transfer: gross trophic processes (bottom-up vs. top-down forcing), appearance of novel resources, the relative importance of specialists vs. generalist consumers, rate of community change (in terms of basic parameters such as species identity, diversity, richness, evenness, and connectivity as well as physical traits like structure, temperature regime, landscape

diversity, etc.), maximum possible home range size, and maximum body size. (See Appendix A for a selection of specific examples across a range of taxa.)

### **Trophic Processes**

The first notable impact following human colonization of new areas has tended to be the extirpation of the megafauna (Barnosky et al. 2004; Terborgh & Estes 2010a). Typically the next community response to human impacts has been the loss of large predators (Terborgh & Estes 2010a) through habitat loss, fragmentation, and direct persecution for the protection of human life and livestock, although reduction in prey numbers through overhunting and competition from domestic livestock can also play roles.

With the loss of top predators, herbivores and mesopredators experience a release (also encouraged by human feeding of free-ranging domestic animals), often with devastating effects on their food supplies (Brashares et al. 2010; Ripple et al. 2010). However, the larger and herd-forming herbivores only have a small window of release before habitat loss and fragmentation first reduce opportunities for migration and then reduce blocks of contiguous habitat below the size required for sustainable populations; extirpating them as well. At this point, the absence of the dominant herbivores may allow vegetation to reach a less exploited state superficially similar to conditions in the presence of top carnivores; especially if increases in mesopredators suppress increases in smaller herbivores.

However, landscapes with adequate refuge areas may experience an explosion of small to medium herbivorous species able to exploit edges and multiple fragmented habitat types (such as the White-tailed Deer that have become a problem in many

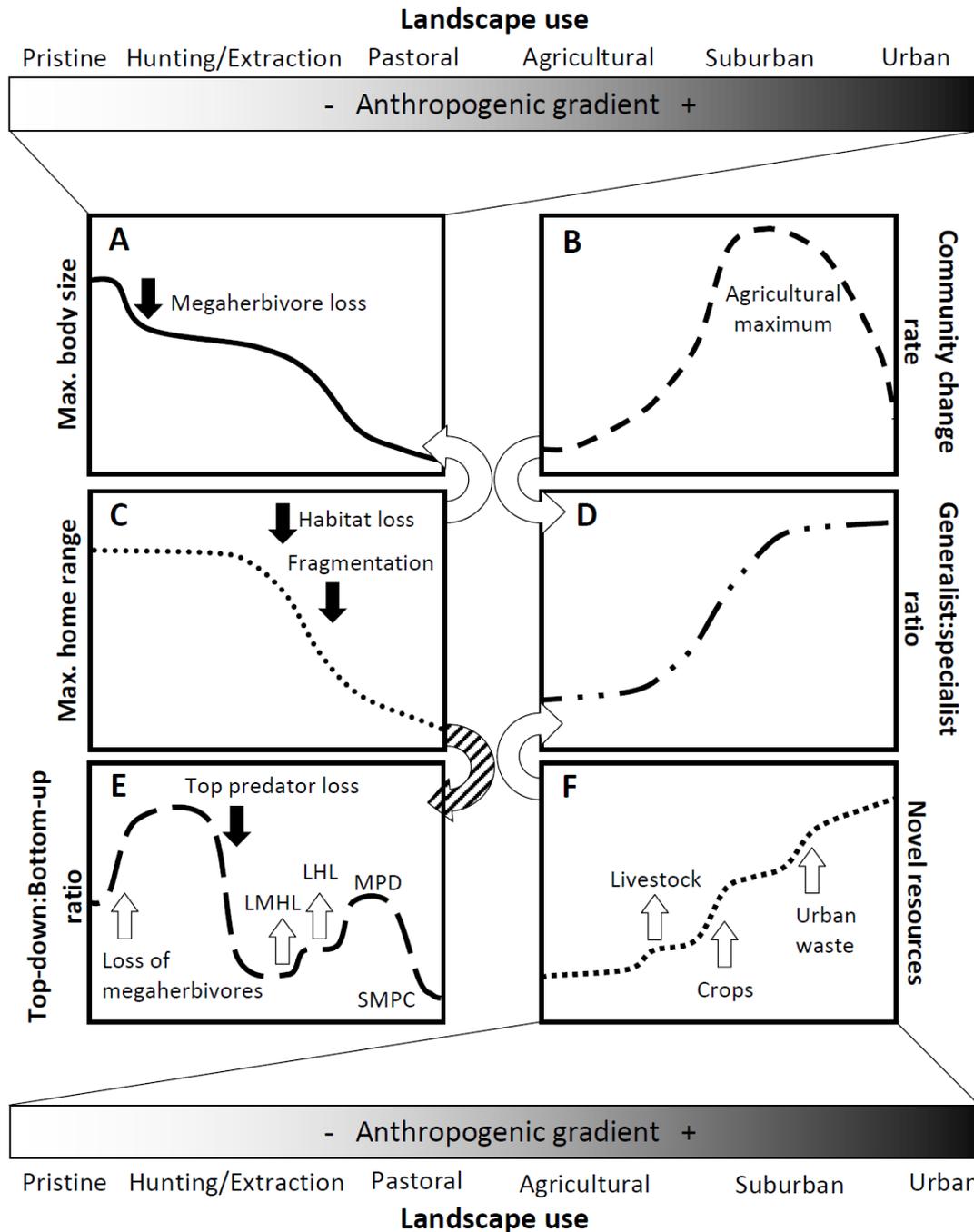


Figure 2-1. Gross trends in community characteristics along the gradient of anthropogenic influence. Arrows indicate influences between community characteristics and influences of events that tend to be concentrated along certain parts of the gradient. White arrows are positive influences; black arrows are negative influences; cross-hatched arrows have different effects in different parts of the gradient. The Top-down:Bottom-up ratio is the relative strength experienced by herbivores. LMHL = Large Migrating Herd Loss. LHL = Large Herbivore Loss. MPD = Mesopredator Dominance. SMPC = Sequential Mesopredator Collapse.

suburban areas in North America; (Ripple et al. 2010) maintaining top-down suppression of the vegetation where they are not squeezed out by denser development. With further urbanization, the larger of the remaining herbivores are lost and mesopredators come to dominate the food web until most of them are lost from the system as well (McKinney 2002).

Thus the gradient of human impact may be characterized by a shifting of dominance between top-down and bottom-up processes (Figure 2-1E). While the shifting between top-down and bottom-up forces is likely to be a general character of anthropogenic influence, the exact placement of the shifts for a given area depends on cultural qualities such as prevalence of hunting and tolerance for wildlife, which affect the viability of the remnant wildlife populations (Terborgh & Estes 2010a).

### **Novel Resources**

Through the gradient of anthropogenic influence, novel resources and opportunities increase: from minor scavenging opportunities around small settlement middens, to domesticated livestock, crops, and introduced exotics providing new foods and new concentrations of food, to surges of productivity caused by increased edge or secondary growth, to the tons of waste produced by industrial societies (Figure 2-1F). The anthropogenic concentration and production of food and waste is tied with habitats being altered or replaced largely through livestock production and agriculture. As biotic communities respond to habitats being fragmented and reduced in area, even resources within fragments change as interior species disappear and edge and exotic species increase.

## **Generalist Omnivores**

While the increasing appearance of novel resources and other community changes are likely to be the death knell for specialists dependent on specific foods, predictable patterns, or stable and unfragmented habitats, they provide vast opportunities for generalists able to take advantage of increased landscape diversity with new resources and habitats (Figure 2-1D; DeStefano & DeGraaf 2003; Fraterrigo & Wiens 2005; Marzluff and Neatherlin 2006; Prange et al. 2004) and the subsequent relaxation of competition from the now extirpated specialist species (Foufopoulos & Ives 1999; Henle et al. 2004). New sources of food are most likely to be exploited by dietary generalists, in particular omnivores. The mesopredators so infamous for being beneficiaries of human disturbance are largely omnivores whose influence on prey numbers is not only increased by lack of top-down suppression by larger predators but also by the avoidance (conferred by omnivory and novel anthropogenic foods) of bottom-up control by prey availability (Brashares et al. 2010).

## **Community Change Rate**

As initial anthropogenic changes lead to community losses and restructuring, those changes themselves likely result in further losses of specialists and relative gains in generalists and exotics (often providing novel resources and/or being generalists themselves; Ruesink 2005) thereby initiating a positive feedback period of rapid increases in community change rate (Figure 2-1B). At some point, the community change rate (however defined) must stop increasing, but it is probably maintained at a higher level in rural anthropogenic landscapes through the rapid seasonal community changes characteristic of agriculture and changes in land use. In more urban areas, biotic community change rate is likely suppressed compared to agricultural areas due to

the permanence of urban structures and land cover compared to the seasonal changes of agriculture.

### **Home Range Size**

As remaining habitat patches become smaller, degraded, and more fragmented, the maximum home range size shrinks and large daily movements are likely to be avoided as they can result in greater contact with humans, both of which reduce maximum supportable body size (Figure 2-1C). This effect is likely to be somewhat mitigated in generalists, which, because of the wide range of resources available to them, can have smaller home ranges than equally-sized carnivores (Harestad & Bunnell 1979) or even some herbivores (*e.g.*, frugivores; Waser 1975). This mitigation is likely to be especially important when human-altered landscapes that are not conducive to wide ranging (because of roads, fencing, quickly changing land cover, and a general intolerance for many types of wildlife) have concentrated novel resources (Bozek et al. 2007; Prange et al. 2004; Tigas et al. 2002).

### **Body Size**

In many anthropogenic landscapes and for many species, the existence of refuges is needed for continued survival (Crooks & Soulé 1999; Livingston et al. 2002). Refuges can serve as areas to avoid persecution or disturbance, areas for breeding, or simply provide space for den sites (Tigas et al. 2002). What can be considered a refuge depends on the body size of the animal. When human-dominated areas are interwoven with extensive natural areas, large bodied generalist omnivores such as wild and feral pigs (Mayer & Brisbin 1991) and baboons (Brashares et al. 2010) can thrive. This occurs where there is small-scale agriculture and small settlements due to low human

population or because larger scale agriculture and settlement are confined, for example, by topography (Tigas et al. 2002; Worman 2010).

However, when human dominance is more complete, these larger species disappear because they are often viewed as pests and cannot persist in the absence of large refuges (Figure 2-1A). Thus in suburban areas, the size of the refuges determines the type of smaller generalist omnivores that can flourish, such as foxes, Raccoons, Opossums (Prange et al. 2004), Brushtail Possums (Hill et al. 2007), and Coyotes (Connolly 1978; Tigas et al. 2002); with the larger-bodied species like coyotes requiring correspondingly larger refuges (Crooks & Soulé 1999; Randa & Yunger 2006). However, usually only the smallest synanthropic generalist omnivores, such as rats, small birds, insects, *etc.*, can thrive in completely urbanized areas (McKinney 2002). This pattern can be seen as a continuation of the anthropogenic sequential collapse in body sizes that begins with the extirpation of the megafauna and ends in series of smaller and smaller mesopredators. The process resembles a Russian *matryoshka* doll that starts as a Woolly Mammoth and ends as a Sewer Rat.

### **Effects on Nutrient Transport**

The predictable effects of human activities on community characteristics are likely to have further effects on nutrient cycling within and flow between ecosystems (Figure 2-2). There appear to be four main ways animal-mediated nutrient transport may be being affected by anthropogenic changes: alteration of its relative importance, a shortening of the average transport distance, a relative increase in nutrient transfers among different habitat types, and a particular directionality of flow.

Sequential anthropogenic changes in trophic structure (by removal of megaherbivores, then top predators, then large herbivores, *etc.*) shift the relative

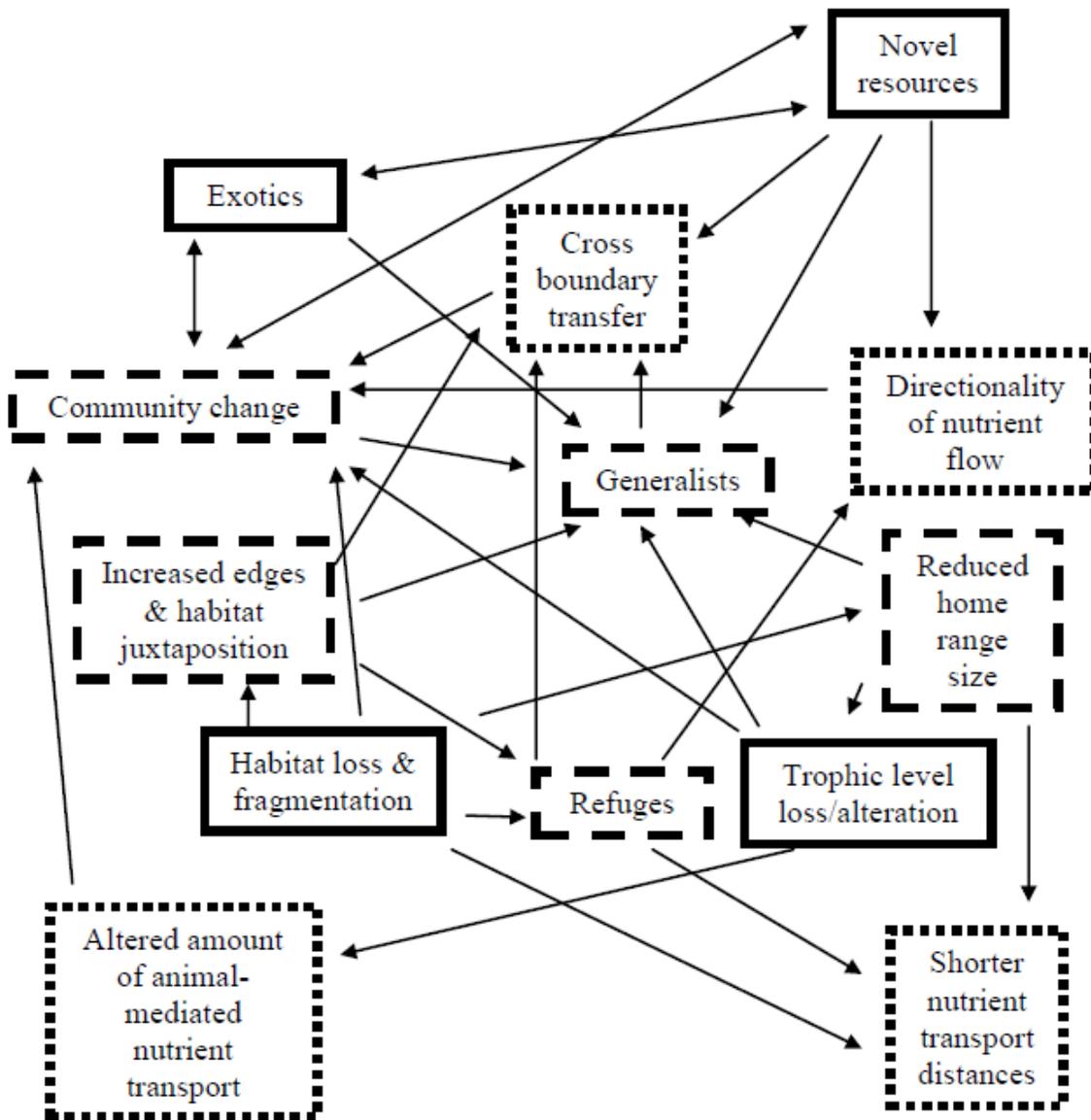


Figure 2-2. Relationships between the direct anthropogenic impacts on biotic communities (solid outline boxes), indirect impacts on biotic communities (dashed outline boxes), and indirect impacts on animal-mediated nutrient transport (dotted outline boxes) discussed in the text. Arrows indicate directionality of influence. For instance, the addition of exotics changes the community and community changes tend to increase vulnerability to exotics.

importance of top-down and bottom-up forces (Terborgh & Estes 2010a). Under conditions when dominant herbivore numbers are largely restricted by predation, there will be a larger standing crop of producer biomass and a correspondingly larger flow of

nutrients through the detrital food web. However, when herbivores are uncontrolled by predation (with predator-proof megaherbivores, a lack of top-predators, or near the end of the sequential mesopredator collapse) a greater fraction of the primary production will be shunted through consumers into the grazing portion of the food web. Under conditions of bottom-up forcing, when consumer numbers are limited more strongly by their food supply than by their predators, it follows that animal-mediated nutrient transfer may become correspondingly more important.

Nutrient transport can be important over both large and small distances (Durbin et al. 1979), for instance, when the nutrients are retrieved from a sink (Vanni & Headworth 2004) or transported from resource-rich zones (Johnston & Naiman 1987), both of which are characteristic of human-impacted areas (Prange et al. 2004). With anthropogenic reduction in home range size, fragmentation of habitats, and hampering of migrations, it is likely that short-range nutrient transport has become relatively more important in human dominated areas. This shift is probably exaggerated by the importance of refuges in matrices that may provide rich foraging opportunities but discourage wide ranging.

The increased complexity of the landscape (more fragmentation and frequent juxtaposition of differing habitat types), the sharpness of edges, the presence of concentrated resources in otherwise undesirable habitats and small refuge areas, and the increased relative importance of generalists less limited by habitat type found in human-dominated areas all suggest that nutrient transfers across habitat boundaries should become relatively more important in disturbed compared to undisturbed areas. This could amplify nutrient ties between systems, especially in severely fragmented

areas. Small patches are unlikely to contain all the requirements for life thus interhabitat movement goes from possible (for generalists) to necessary.

Because of this necessity, foraging often involves ranging outside refuges and nutrients sequestered from feeding habitats may be concentrated in refuges. This will be especially true in areas where novel resources are concentrated in areas (such as an agricultural field or garbage dump) that are unsuitable for other uses. It seems likely that the overall animal-mediated flow of nutrients in anthropogenic landscapes is primarily into refuge areas largely from novel resources outside of the refuges. This flow may eutrophy the soil or water in the refuges making invasion by exotic species more likely, encouraging further community change in the patches that remain.

Interestingly, while generalists are likely to be favored in multiple ways by anthropogenic habitat alteration, it seems that their direct and indirect roles in altering nutrient flow patterns in anthropogenic landscapes are probably largely because they are an increasingly dominant guild in the community rather than because of inherent generalist qualities. The primary way inherent generalist qualities influence nutrient transfer is through the ability to use a diversity of habitats and thus transport nutrients from one system to another (Figure 2-2). Otherwise, their importance to nutrient regime changes may be simply because they are the primary type of animal able to survive in human-modified landscapes and thus become the guild primarily responsible for nutrient flows that would be directly or indirectly modified anthropogenically, even if a community were composed entirely of specialist species.

### **Conclusion**

It is likely that the altered animal-mediated nutrient flows created by anthropogenic influence are characterized by short-range, inter-habitat transfers with a net flow into

refuge areas. Generalist omnivores are likely principal players primarily because they benefit from or are resistant to many anthropogenic changes far more than specialists and thus increase in dominance in disturbed landscapes. Inter-habitat transfers, however, do seem likely to be increased by generalists specifically, as generalists are more likely to incorporate multiple habitats in their daily routines.

Of course, the overall pattern of nutrient flow in an anthropogenic landscape will often be dominated by human inputs and concentrations. Eutrophication through fertilization and pollution and the concentration of nutrients from agricultural areas to urban areas have replaced long-distance animal-mediated nutrient transfer over large swaths of the globe. However, within the human-dominated landscape, it is likely that animal-mediated transport is important in redistributing nutrients from anthropogenic sources into nearby refuge areas, especially when bottom-up forces dominate. These sorts of changes in nutrient flow patterns may make habitat management and restoration even more challenging as habitat remnants receive influxes of anthropogenically-derived nutrients from high densities of generalist species supplemented with novel resources. This eutrophication of habitat patches will likely result in upsetting the competitive interactions of the flora and encourage invasion by exotic species, putting native species and communities at further risk. The ways in which anthropogenic community changes alter animal mediated nutrient flows have been neither much studied nor quantified, yet they have potentially broad impacts on the functions of ecosystems worldwide and thus need to be further addressed.

## CHAPTER 3 TOP-DOWN EFFECTS OF A GENERALIST OMNIVORE MEDIATED THROUGH LANDSCAPE PATTERNS

### **Introduction**

The relative importance of top-down and bottom-up forces in structuring communities has a long history of description and debate (Ehrlich & Birch 1967; Hairston et al. 1960; Oksanen & Oksanen 2000; Polis et al. 2000; Power 1992; Slobodkin et al. 1967; Terborgh 2010; Terborgh & Estes 2010b; Terborgh et al. 2001). Increasingly it is becoming clear that the loss of large predators and the subsequent increases in the numbers and boldness of the consumers that are their prey have ramifications that reach much further than merely reducing the standing crop of producer biomass. Increases in the abundance of consumers at intermediate trophic levels can impact ecosystem properties as diverse as disease dynamics, nutrient cycles, vulnerability to invasives, fire regime, species richness, and species diversity (Daskalov et al. 2007; Estes et al. 2011; Holdo et al. 2009; Maron et al. 2006; Pace et al. 1999; Paine 1980; Terborgh & Estes 2010b; Terborgh et al. 2001). Moreover, many such consumers are mobile, implying that such shifts can ramify across landscapes. With the loss of predators and a subsequent increase in bottom up control, landscape processes, such as landscape supplementation (when additional resources occur in different habitat) and complementation (when needed resources occur in different habitats) (Dunning et al. 1992), are likely to be altered and often become more important as the impacts of consumers released from predation spread across landscapes. Comparable effects can arise when consumers are introduced into environments lacking predators and parasites.

Some of the more globally successful vertebrate consumers in the face of anthropogenic change are members of the Superfamily Suiodea, pigs and their relatives (Graves 1984). These taxa can be key drivers mediating anthropogenic effects on ecosystem properties over the areas of the Earth in which they occur (Bratton 1975; Nogueira-Filho et al. 2009; Roemer et al. 2001). Their size and defense capabilities limit their vulnerability to mesopredators (except for a few instances of mesopredators acting in packs, *e.g.*, dingoes; Newsome 1990). This group of consumers is not only often subjected to strong landscape complementation because of its requirement for permanent water sources (see below) but, because its members are mobile opportunistic generalists, they also likely often benefit strongly from landscape supplementation, magnifying their impacts on local habitats and patches (a neighborhood effect). In this paper, after sketching some key traits of suiods that enhance their ecological effects, we present an observational and experimental study of their impacts on herbaceous plant communities in coastal Florida.

### **Suiod Traits as Drivers of Ecological Patterns**

Swine and peccaries (Superfamily: Suiodea) have an unusual foraging strategy of rooting for animal and vegetable matter, as well as foraging on aboveground resources. This ability to access hidden resources as part of an omnivorous diet has likely contributed to their successes both as native faunal components on most continents and as exotic invasives of global importance (Graves 1984; Oliver & Brisbin 1993). Native species of pig (Family: Suidae) are found in scrub and non-boreal forest habitats over most of Eurasia and North Africa (Oliver et al. 1993). The tropical forests of the Malay Peninsula and islands of Southeast Asia hold nine species (Duff 2004) and were likely a center of pig evolution (Larson et al. 2005). Native pig species are also present

in most of sub-Saharan Africa in forests, bush, and open habitats (Kingdon 1979).

Peccaries (Family: Tayassuidae) are found mostly in tropical forests and scrub of South and Central America, with one species extending up to the deserts and scrublands of southwestern North America (Sowls 1997).

While native suoid species cover much of the Earth's habitable land mass, Australia, most of North America, and most oceanic islands were devoid of suoids for most of the Holocene until pigs (mostly *S. scrofa*) were widely introduced by humans (Oliver & Brisbin 1993). These introductions were often domesticated pigs that either escaped or were deliberately managed as free-ranging livestock. However, in some cases, exotic populations were established either by the introduction of true Wild Boar or the transportation of Feral Hogs from one area to another to facilitate hunting (Cuevas et al. 2010; Graves 1984), a process which still occurs (Hampton et al. 2004a). (Feral Hogs are defined to be animals whose ancestors were domesticated pigs that escaped captivity and subsequently readapted to the wild. Morphologically they are intermediate between wild and domestic *S. scrofa*; Mayer & Brisbin 1991.) Wild Boar have also in several instances reestablished previously extirpated populations by escaping from captivity (Goulding 2001; Welander 2000).

If suoids as an agent of disturbance have long been part of the selective environment of a plant community, one would expect species in that community to have evolved various adaptations to help cope with such disturbance; all species without such adaptations will have been filtered out of the community. Although their characteristic rooting behavior has important impacts on the vegetation in areas where suoids are native (Ickes et al. 2001), rooting in naïve ecosystems can be truly

devastating (Hone 2002; Nogueira-Filho et al. 2009; Vitousek et al. 1997a). Rooting allows access to subterranean plant storage organs, fungus, and animal foods not readily available to most animals, which contributes to the flexible omnivorous diets of these consumers. These extra resources doubtlessly bolster the extremely high hog densities in some areas (from 2 pigs/km<sup>2</sup> in Australia to 37 pigs/km<sup>2</sup> in Hawaii, resulting in ~130 and 1870 kg of pig biomass/km<sup>2</sup>, respectively; Saunders & McLeod 1999). The destructive potential of suoid rooting on plant communities is magnified by these high population densities and by the fact that suoids often forage in large groups, systematically devastating swaths of turf. The effects of exotic hogs as major disturbance agents on plant communities have been described in diverse ecosystems from deserts (Cuevas et al. 2010) to Mediterranean-climate grasslands (Kotanen 1995) to tropical rainforests (Nogueira-Filho et al. 2009) to sub-alpine grasslands (Hone 2002).

Another suoid characteristic that affects, and at times constrains, their ecological impacts is their physiological dependence on wallowing for cooling and the maintenance of a healthy skin condition, including the removal of ectoparasites (Graves 1984). Suoid wallowing involves bodies of water or mud, which is thus quite different from the dust bathing of many other species (which is often also called wallowing). Because the need for wallowing ties most suoids to permanent access to water and shelter from the sun is necessary for heat balance (Huynh et al. 2007; Kingdon 1979), landscape complementation is likely to be particularly important to understanding the magnitude of suoid impacts (Adkins & Harveson 2007; Baber & Coblentz 1986; Choquenot & Ruscoe 2003; Ickes et al. 2005). Even in areas (or times; Baber & Coblentz 1986) with widely available water, landscape supplementation of resources from neighboring habitats may

need to be taken into account to understand the impacts suoids have on their habitat. Most prior studies have concentrated on measuring the physical damage caused by hogs and ignored the potential influence of landscape structure (including the interactive effects of supplementation and complementation) on the location and magnitude of hog impacts.

### **Impacts in Coastal Florida**

This study investigates the importance of landscape patterns in determining Feral Hog impacts in coastal Florida. This region today lacks a top predator of Feral Hogs (except for occasional human hunters). Hogs were first released in Florida by the Spaniards, and are abundant with effects that are obvious to even casual observers in many communities (pers. obs.; Abrahamson & Hartnett 1990; Engeman et al. 2003; Mayer & Brisbin 1991). Our focus is on how consumption and rooting disturbance by Feral Hogs influences the structure of understory herbaceous plant communities. Our techniques in particular use exclosures and simulated rooting to mimic hog disturbance. To address the importance of landscape context on this interaction, we compare herbaceous communities on islands of coastal hammock forest embedded in an important feeding habitat (tidal marsh), with herbaceous communities in comparable coastal forest on mainland peninsulas adjacent to the marsh. Field observations have shown that Feral Hogs forage considerably in coastal marshes, yet these hogs also utilize forest habitats for nesting and wallowing as well as foraging (unpub. data). The effects of landscape complementation and supplementation should be particularly strong on the islands, completely surrounded by the marsh foraging habitat. We hypothesized that hogs overall decrease herbaceous species richness, cover, and biomass, in both landscapes, and moreover that hog impacts would be greater on the

islands because of their increased integration with the marsh feeding areas. This integration should result in the islands providing a more productive foraging landscape while still providing nesting and shade opportunities and therefore should be more heavily used and impacted by the hogs.

## Methods

### Study Site

The Lower Suwannee National Wildlife Refuge (214 km<sup>2</sup>) is on the west coast of Florida (29° 17' N, 83° 10' W), centered on the mouth of the Suwannee River on the west coast of northern peninsular Florida. The study site is located in a portion of the refuge south of the river in the coastal region (Figure 3-1). The region of the site was chosen for this study because of a combination of accessibility (by road and boat), and because the landscape contained both a number of hammock islands in the marsh and nearby hammock mainland areas. The coastline is rimmed by a slightly brackish tidal marsh (1-2 ppt) fed by the Suwannee River and California Swamp. The marsh is dominated by the fresh/brackish water Saw-grass (*Cladium jamaicense*) and Black Needle Rush (*Juncus roemerianus*). A somewhat salt-tolerant species, *J. roemerianus* extends more seaward than *C. jamaicense*, which lines creeks and hugs the coastal hammocks. American Bulrush (*Schoenoplectus (Scirpus) americanus*) is found in less densely vegetated areas with a disturbed and looser substrate. The bulrush areas are heavily used by the pigs, and are likely maintained by and may even result from pig rooting (Figure 3-2; CW pers. obs.). Preliminary dietary analyses (presented in more detail elsewhere) suggest that the pigs garner considerable food resources from the marsh environment. The complex boundary between the coastal hammock and the marsh allows these three marsh plant species to form a mosaic of monodominant

patches. There are also a few small (~ 10 m<sup>2</sup>) evaporation pools bordering coastal hammocks that are dominated by Spike Grass (*Distichlis spicata*).

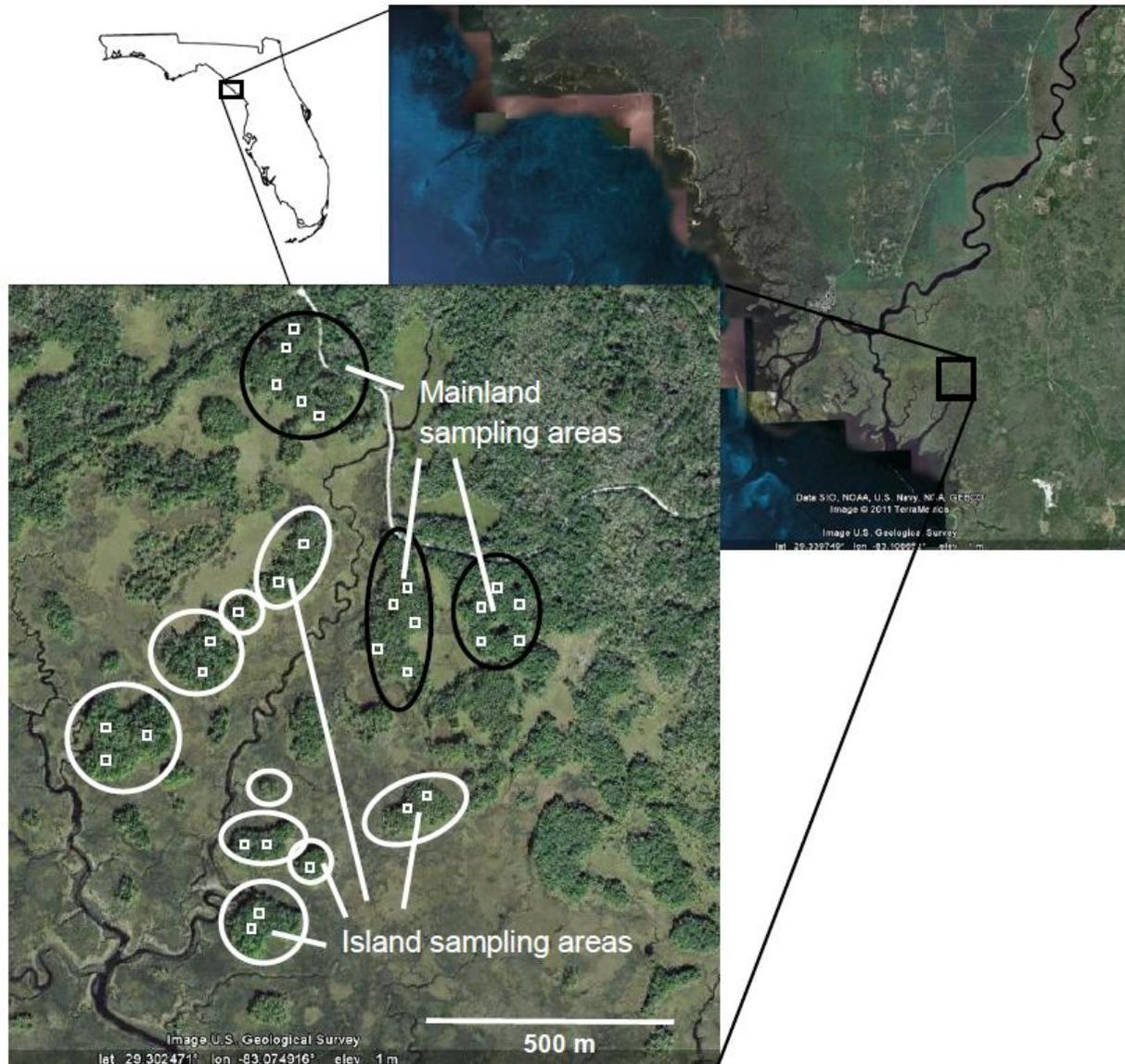


Figure 3-1. An overview of the study site in the Lower Suwannee National Wildlife Refuge, Florida. Coastal hammock “mainland” and “island” sampling locations for this study are indicated. Locations of plot sets are indicated by squares.

The coastal hammock bordering the tidal marsh is characterized by Eastern Red Cedar (*Juniperus virginiana*) and Cabbage Palm (*Sabal palmetto*), with oaks (*Quercus*

sp.) and planted native pines (*Pinus* spp.) also being common. The subcanopy is dominated by Yaupon Holly (*Ilex vomitoria*), Dahoon Holly (*Ilex cassine*), bay (*Persea* spp.) and, in the drier areas, Saw Palmetto (*Serenoa repens*). In addition to the mainland, the coastal hammock is also found on small (~1000-12,000 m<sup>2</sup>) forested islands that are more integrated into the tidal marsh than are the mainland areas (Figure 3-1). The amount of herbaceous undergrowth varies greatly from none in the wettest areas to complete cover in the areas least subjected to flooding.



Figure 3-2. A time series of a bulrush area in the tidal marsh, Lower Suwannee Wildlife Refuge, Florida. Note the same palm snag in the distance. The foreground is an area of American Bulrush, the background is Black Needlerush, the tip of a Sawgrass area is seen on the right, and islands of coastal hammock are in the far background. A) The winter of 2005. B) The area was freshly rooted in the spring of 2010. C) The spring of 2011. D) A portrait of the porcine perpetrator actively rooting in a different bulrush area in the spring of 2010.

A number of mid-sized mammals can be found in these habitats. In particular, the Nine-banded Armadillo (*Dasypus novemcinctus*), Virginia Opossum (*Didelphis virginiana*), and Raccoon (*Procyon lotor*) are common in the coastal hammock including the islands. Less common are the Coyote (*Canis latrans*) and Bobcat (*Felis rufus*), the latter of which is known to travel through the marsh to visit the coastal hammock islands. White-tailed Deer (*Odocoileus virginianus*) are rare but present throughout the coastal hammock including the islands. Feral Hogs (*Sus scrofa*), however, are extremely common, compared to the other species, and moreover are long-term residents, having been introduced to Florida almost 500 years ago by Hernando de Soto (Mayer & Brisbin 1991).

The study area comprised sampling areas within 3 coastal hammock areas of the mainland and 8-10 islands (depending on the analysis) on either side of Barnett Creek. All of these areas were within 1.25 km of each other (Figure 3-1). These sampling areas were selected based on accessibility, proximity, and habitat.

## **Study Design**

### **Feral Hog rooting**

An index of the extent of Feral Hog rooting was measured at the end of each season (spring, summer, fall, and winter) from the summer of 2005 to the fall of 2006 by observing rooting within 1 m of either side of 50 m line transects. The rooting-adjacent distances were summed for each transect and those sums were averaged for the islands and the mainland to form the index. A total of 25 mainland transects were measured each time: 5 for the western portion of the mainland and 10 each for the middle and eastern portions. The numbers of mainland transects were based roughly on the length of marsh boundary in each area. A total of 30 transects were measured

on the islands each sampling period. The number of transects measured on each island varied from 1 to 5, depending on island size. The percent of the areas rooted was estimated by measuring the length of the line transects that traversed rooted areas and dividing by the total of the transect lengths. Due to the non-normal distribution of the data, the distances rooted for the mainland and islands were compared using a Wilcoxon sum rank test for each season.

### **Exclosures**

Rooting is only the most visually obvious impact of hogs on the herbaceous community. They also trample, browse/graze, and deposit nutrients; all of these processes could affect the herbaceous community through direct and indirect mechanisms. To assess the cumulative impact of Feral Hogs on herbaceous plants, experimental manipulations were carried out within 30 sets of 4 m x 4 m plots: 15 sets on the mainland and 15 on the islands. Five sets were placed in each of the three mainland areas. The number of plot sets per island varied from 1-3, depending on the size of the island. The plot sets were placed to best maximize the spacing between the plot sets while still being reasonably representative of the herbaceous community in the area. This semi-systematic approach was chosen due to the difficulties of purely random placement of multiple plot sets in small areas. These difficulties include plot sets overlapping with each other, extending into the marsh, not representing the typical herbaceous community types in an area, or not placed so all three plots could share similar communities.

Each set consisted of three plots: a control, an exclosure, and a tilled plot (to mimic increased hog rooting). The exclosures were built to encompass square 4 m x 4 m areas. They were constructed with 3' hog wire fencing, metal u-posts at the corners,

and a wooden stake in the middle of each side (Figure AB-1). After an exclosure was built, out of the four adjacent 4 x 4 m areas, the two were chosen that qualitatively most resembled the exclosure in terms of the herbaceous communities. Of the two adjacent plots, one was assigned randomly for till treatment and the other served as the control. A till treatment was included to explore the effect of increased physical disturbance on the herbaceous community. The external plots were given a 1 m buffer zone from the exclosure. Tilled plots were lightly tilled with a hand-hoe every six months starting in December 2007 (three months after the exclosures were established) until December 2008 to a depth of ~5-10 cm to mimic the physical disturbance of hog rooting. The presence of fresh hog rooting in the non-exclosure plots was noted opportunistically throughout the study. Hog rooting and armadillo rooting were clearly distinguishable based on size and geometry of the disturbance.

Herbaceous vegetation surveys were done in each plot every six months (3 months offset from the tilling of the tilled plots) from fall 2007 to spring 2009 and one final time in the fall of 2010. Herbaceous species richness (including morphospecies) in the plots was recorded in each sampling period. Specimens were taken to the University of Florida Herbarium for identification by herbarium staff. In some cases, it was impossible to identify specimens to species because only non-reproductive individuals were available for collection. Herbaceous cover was estimated using the point method (Goodall 1952) with five evenly spaced points in four evenly spaced rows in each plot. Vegetation was scored separately in 25 cm height increments up to a height of 1 m for each point.

In the spring of 2011, at the end of the field study, aboveground plant samples were harvested to estimate living aboveground biomass of the herbaceous community in the plots (Figure AB-2). Due to its destructive nature, biomass sampling could only be done once over the course of the study. For plants with partly woody stems (e.g., *Smilax* spp. and *Rubus* spp.) only the herbaceous portions were taken to prevent the dead woody mass from influencing the results. For safety reasons, Poison Ivy (*Rhus radicans*) was not sampled. Though somewhat widely spread among the plots (*Smilax* and *R. radicans* especially) these taxa were always at very low density and it is reasonable to presume that they contributed little to the overall biomass of the plots.

For plots in which the biomass was sparse, the entire aboveground living herbaceous biomass was taken. In more thickly vegetated plots, a subsample of the biomass was taken sequentially from non-overlapping randomly placed 1 m x 1 m quadrats until enough biomass had been collected for laboratory analysis of nutritional content (not presented here). In plots with extremely rank growth, 0.25 m x 0.25 m quadrats were sampled, as harvesting everything from a 1 m x 1 m plot would have been impractical. The samples were dried at 50° C and weighed to estimate above ground living herbaceous biomass.

For species richness, cover, and biomass, the effect size of the treatments were calculated by subtracting the cumulative changes in the control from the cumulative changes in the paired treatment plots. 95% confidence intervals were established by bootstrapping 10,000 times. In cases that were consistent with predictions, the confidence intervals are one-tailed, otherwise, they are two-tailed. If the confidence intervals did not overlap zero, the effect was deemed significant.

The species composition of the herbaceous communities of the islands and mainland were compared by summing the total number of times a species appeared during the vegetation surveys for island plots and also for mainland plots. The frequencies of each species in the two different location types were compared with  $X^2$ . Issues of multiple comparisons apply if the existence of at least some significant difference is of interest (which is not the case here) but not if the comparisons are used to be informative about the occurrence pattern of any single species. However, if the overall difference between the island and mainland communities is of interest (as is the case), multiple comparisons do not present a conceptual difficulty, as Type I errors should not be biased in producing false positives for either location type. False positives should reduce the detected difference between the islands and the mainland, making uncorrected comparisons more conservative. Therefore, species occurrence results are presented with and without Šidák's correction for multiple independent tests (Šidák 1967).

### **Landscape composition**

The landscape context for the mainland and island study areas was determined by measuring the percent covered respectively by hammock, bulrush areas of the marsh, and the marsh excluding bulrush areas in 50 m segments along 1 km transects using aerial photography provided by Google Earth and ground-truthed. (Nearest-neighbor distances between islands within a 1 km radius of the study site were determined as well.) Transects into the marsh were placed in the four cardinal directions around each island. As there were 3 mainland areas and 9 islands, each mainland area was sampled three times to equalize sample sizes with each cardinal direction sampled by three evenly spaced transects per mainland area.

For the directions in which the mainland hammock areas were contiguous with the coastal forest, a pseudo-boundary of the sampling area, and transect starting point, was set 25 m away from the furthest out enclosure. This corresponds to the overall average distance from enclosures to their nearest marsh edge. Otherwise, the boundary between hammock and marsh was used as the transect starting point.

The transects were 1 km in length so as to enclose the length of the major axis (0.70 – 0.75 km) of daily ranges of Feral Hogs in a similar tidal marsh system (Wood & Brenneman 1980). This distance should therefore include the habitat available in a typical foraging day for a hog based in each hammock area.

The average percentage of each habitat in 50 m segments along the transects (given in Figure 3-3) was converted to an index of area for the bulrush feeding areas by squaring the average distance from the hammock for each transect segment and subtracting the square of the next shorter distance to give the relative area represented by each 50 m segment. Then the relative area was multiplied by the average percentage of bulrush found in each segment to give the relative areas covered by bulrush at each distance from the hammocks. The area index was summed with those of shorter distances to give a cumulative area index. This index gives the relative availability of bulrush within a given distance of the island and mainland hammock areas. The ratio of the island and mainland cumulative area indices for the bulrush feeding areas is comparable to the ratios of the island to mainland hog density indices (see below). 95% confidence intervals for the ratio were established by bootstrapping to determine at which distances the ratio deviated from 1.

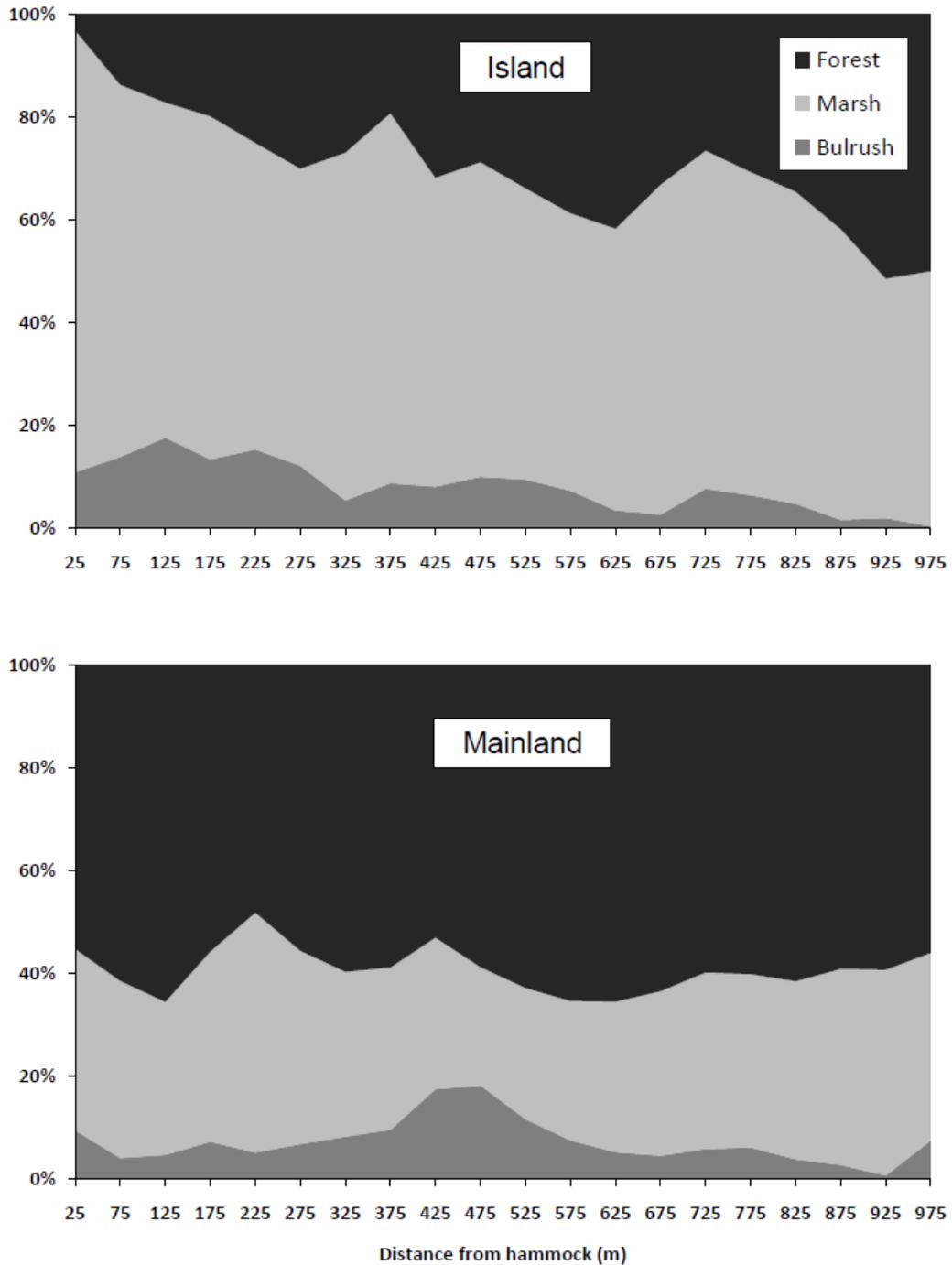


Figure 3-3. The major habitats surrounding the sampled island and mainland hammock areas. The bulrush areas used for feeding by the Feral Hogs are indicated separately from the rest of the marsh. Note that the marsh area is constant with distance from the mainland areas but increases closer to the islands giving the islands greater access to the marsh. Note also that the peak of bulrush extent is closer to the island hammocks than the mainland hammock.

## **Relative densities**

Relative hog densities for the mainland area and the island areas were established by compiling opportunistically gathered data into three indices: direct encounters, hog remains, and hog nests.

Encounters in the marsh were assigned to the closest hammock area. Reencounters with the same individuals in the same day were not counted.

Hog remains were never found more than 10 m from a hammock. Remains were considered to be from the same individual if they were found within ~20-30 m of each other, were consistent in size and age, and did not repeat skeletal elements.

Nests were constructed by the hogs gathering pine needles, palm fronds, or other detritus into oval rings averaging 2 m x 1.5 m x 0.2 m. Nests were counted if they appeared to be fresh and had not been counted before.

Because the islands were accessed by passing through the mainland areas, the three opportunistic indices are likely biased towards the mainland. Therefore, an unbiased index was calculated based on systematic hog fecal counts made in 50 x 2 m plots (26-30 island plots and 25 mainland plots). The counts were done every season from the summer of 2005 until the fall of 2006 with an additional sampling in the winter of 2008-2009. New plots were used for each season. Piles of feces, defined as a cluster of fecal pellets of similar size and apparent age within 0.5 m of each other, were counted in the plots. Because the fecal decay rate was extremely low (50% survival to 471 days), changes over time could not be examined.

## **Results**

The amount of rooting varied widely among locations within a season and also varied widely among seasons for a single location. Transects on the mainland had

significantly more hog rooting than did those on the islands in the 2005 seasons (Wilcoxon sum rank test, all  $p \leq 0.001$ ). The mainland area was estimated to be 6, 9, and 3% rooted in the summer, fall, and winter of 2005, respectively. In the same time periods, the islands were estimated to be 1, 1, and 0.3% rooted. However, in 2006, rooting in the hammocks plummeted (mainland spring, summer, and fall: 0.44, 0.12, and 0.08%; island: 0.04, 0.39, and 0.46%) and no significant differences were found between the islands and the mainland (Figure 3-4).

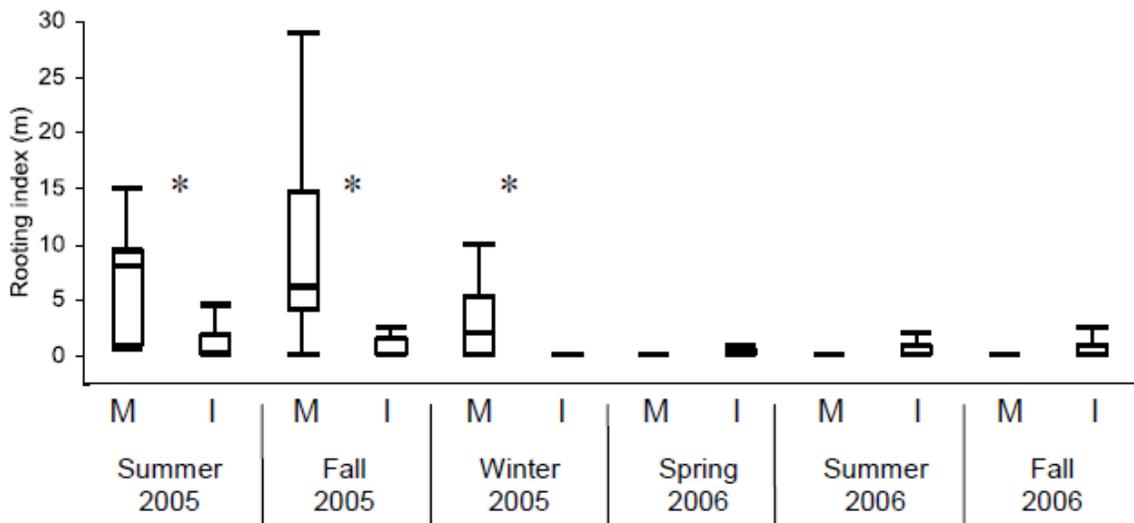


Figure 3-4. Feral Hog seasonal rooting activity in a coastal hammock community on the mainland (M) as well as isolated hammock islands (I) in the tidal marsh in the Lower Suwannee National Wildlife Refuge, Florida. Seasons in which there were significant differences are marked “\*”. The lines in the boxes indicate the medians, the boxes indicate the 25<sup>th</sup> and 75<sup>th</sup> percentiles, and the whiskers indicate the last sample within 1.5 times the interquartile distance.

One unexpected result of the study was that experimental manipulation could positively influence hog behavior. Tilling increased the chance of hog rooting compared to control plots. In 74 instances of hog rooting in plots, 50 were observed in tilled plots and 24 were in controls ( $\chi^2 = 9.1$ ,  $df = 1$ ,  $p = 0.002$ ). Additionally, tilling increased the

average extent of rooting in the plots that were rooted (tilled: 23% rooted; control: 11% rooted; Wilcoxon sum rank test:  $S = 666.5$ , one-tailed  $p = 0.007$ ). In a paired comparison in which at least one of the two plots for each location was rooted, tilled plots had on average 16% more of their area rooted than did their respective controls (Wilcoxon signed rank test:  $S = 563.0$ ,  $p < 0.0001$ ).

The overall average herbaceous species richness in controls was greater in the mainland controls ( $\bar{x} = 7.0$  species/16 m<sup>2</sup> plot, SD = 3.8, range = 0 – 17 sp./plot) than in the island controls ( $\bar{x} = 3.2$  species/16 m<sup>2</sup> plot, SD = 2.5, range = 0 – 13 sp./plot; Wilcoxon sum rank test:  $S = 7361$ ,  $p < 0.001$ ). The response of species richness to the treatments was different on the islands and the mainland. There was no detectable effect of the exclosures compared to controls but an immediate and temporary effect of the tilling on herbaceous species richness in the island plots. However, on the mainland, there was a significant and asymptotic increase in species richness in the exclosures (~1.6 species/16m<sup>2</sup> plot) compared to controls and a lagged decrease in the tilled plots (-2 species/16m<sup>2</sup> plot) and subsequent recovery 15 months after tilling was ceased (bootstrapped 95% confidence intervals are shown in Figure 3-5).

Herbaceous cover showed similar patterns to species richness. Overall, cover in controls was higher on the mainland ( $\bar{x} = 30\%$ , SD = 0.30, range = 0 – 95%) than on the islands ( $\bar{x} = 19\%$ , SD = 0.24, range = 0 – 75%). The exclosures had no detectable increase in herbaceous cover on the islands but a slight possibly asymptotic increase on the mainland (~6%) compared to controls; however this was only significant in one month. Tilling had a negative effect in both areas compared to controls, but a stronger

impact on the mainland (island: -5%; mainland: -21%) with little or no apparent recovery a full 15 months after tilling ceased (island: -6%; mainland: -14%; Figure 3-6).

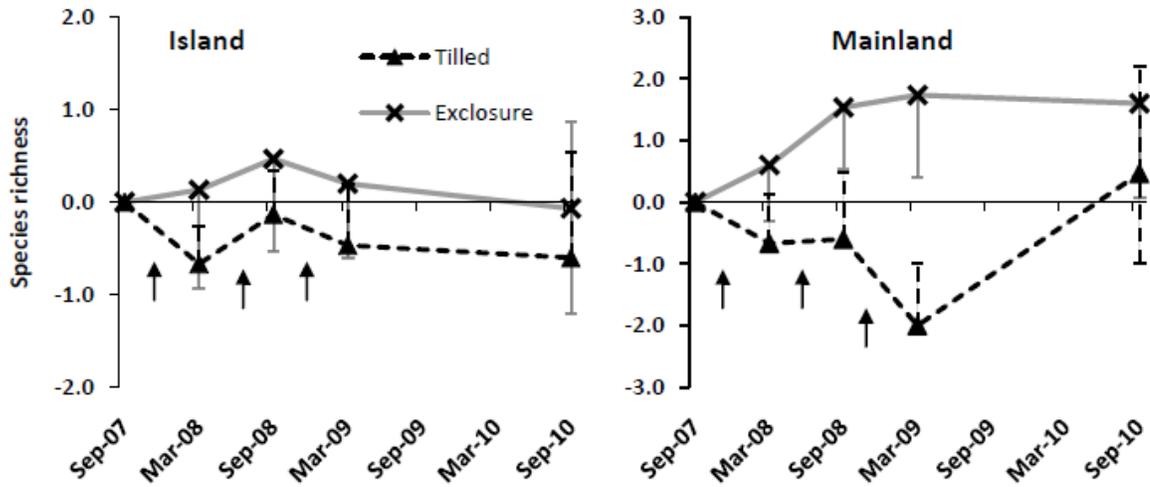


Figure 3-5. The effects of Feral Hog exclosures and artificial rooting relative to paired controls on the herbaceous species richness in a coastal hammock community on the mainland as well as isolated islands in the marsh in the Lower Suwannee National Wildlife Refuge, Florida. Tilling treatment times are indicated with arrows. 95% confidence intervals are indicated.

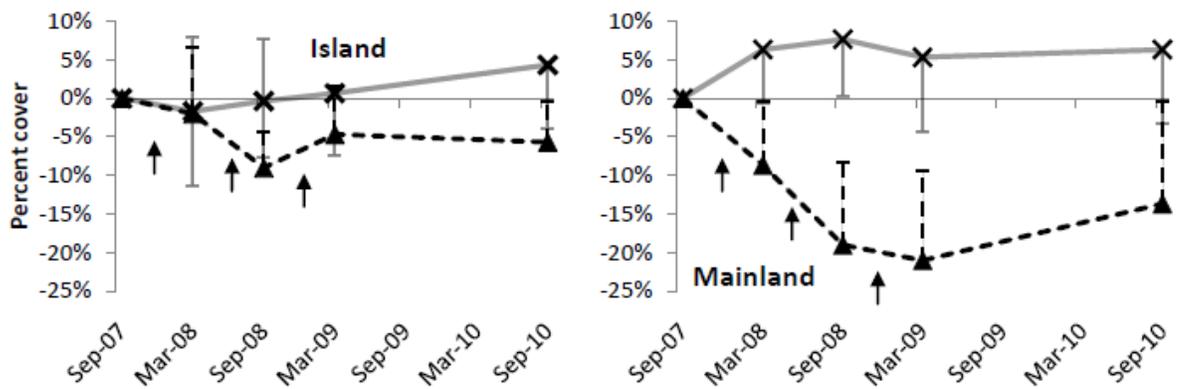


Figure 3-6. The effects of Feral Hog exclosures and artificial rooting relative to paired controls on the herbaceous cover in a coastal hammock community on the mainland as well as isolated islands in the marsh in the Lower Suwannee National Wildlife Refuge, Florida. Tilling treatment times are indicated with arrows. 95% confidence intervals are indicated.

Herbaceous biomass was higher in the mainland controls ( $\bar{x} = 7.7 \text{ g/m}^2$ , SD = 9.4, range = 0.1 – 28.7  $\text{g/m}^2$ ) than in the island controls ( $\bar{x} = 3.9 \text{ g/m}^2$ , SD = 5.0, range = 0 – 16.4  $\text{g/m}^2$ ). Tilled plots on the islands had reduced biomass compared to their controls (-1.4  $\text{g/m}^2$ ) while tilled plots on the mainland were not significantly different from their controls 15 months after tilling had ceased. Exclosures on both the islands and mainland had similar increases in biomass compared to their controls (island: 13.5  $\text{g/m}^2$ ; mainland: 12.9  $\text{g/m}^2$ ; Figure 3-7, Figure AB-3).

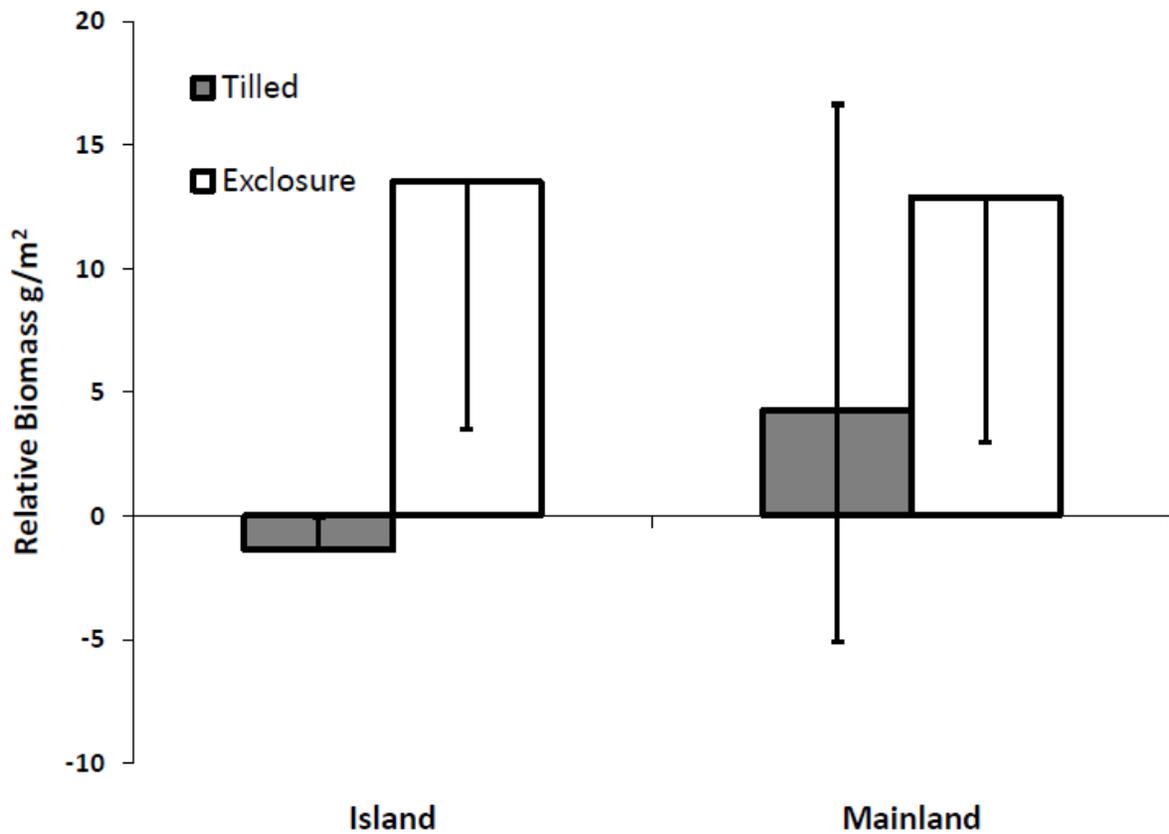


Figure 3-7. The effects of Feral Hog exclosures and artificial rooting on the herbaceous biomass in a coastal hammock community on the mainland as well as isolated islands in the marsh in the Lower Suwannee National Wildlife Refuge, Florida relative to paired controls. The biomass was collected after 3.5 years of exclosure treatment and 21 months after tilling was ceased. 95% confidence intervals are indicated.

Out of 56 herbaceous species, 54 were found on the mainland, while only 39 were found on the islands (Table 1). Note that the area sampled is equal for the mainland and islands. Of these 56 species, 32 were found more frequently in the mainland plots than on the island plots ( $4.0 < X^2 < 68.2$ , all  $p < 0.04$ ), 22 were found with equal frequency in both areas, and only 2, Spanish Dagger (*Yucca aloifolia*) and a vetch (*Vicia* sp.), were found more frequently in the island plots ( $X^2 = 5.0$ ,  $p = 0.025$  and  $X^2 = 8.0$ ,  $p = 0.004$ , respectively). With a Šidák's correction for multiple comparisons, 16 species were found more frequently on the mainland, 40 were found with equal frequencies, and none were found more frequently on the islands. In either case, significantly more plant species had higher frequencies on the mainland than on the islands ( $X^2 = 26.5$ ,  $p < 0.0001$ ;  $X^2 = 16$ ,  $p < 0.0001$ ; respectively).

The 95% confidence intervals of the cumulative bulrush area index ratio did not include 1 for distances of 100 to 300 m from the hammock edge; indicating that greater bulrush area is accessible from the islands than from the mainland in that distance range. In that range, the islands provided access to an average of 2.8 times (range: 2.3 – 3.4) the area of bulrush habitat as the mainland did. At no distance did the mainland provide more access than the islands to bulrush feeding areas (Figure 3-8).

Nearest-neighbor distances between islands averaged 55 m and ranged from 10 to 273 m, within the zone of bulrush advantage when foraging from the islands compared to foraging from the mainland.

Relative hog densities averaged 3.4 times higher in the island/marsh than in the coastal mainland ( $6.1 < X^2 < 420$ , all  $p < 0.01$ ; Table 3-2). The unbiased fecal count index was 4.4 times higher in the island/marsh than on the mainland (Figure 3-9).

Table 3-1. The herbaceous species contained in the study plots, their occurrences in the plots on the islands and mainland, and which area, if any, had significantly more occurrences.

Common name	Latin name	Family	Occurrence (225 max)		
			Island	Mainland	More?
Beaked Panicgrass	<i>Panicum anceps</i>	Poaceae	132	126	
St. Augustine grass	<i>Stenotaphrum secundatum</i>	Poaceae	79	153	M**
Poison Ivy	<i>Toxicodendron radicans</i>	Anacardiaceae	67	124	M**
green briar	<i>Smilax</i> sp.	Smilacaceae	82	103	
fimbry	<i>Fimbristylis</i> sp.	Cyperaceae	72	107	M
marsh pennywort	<i>Hydrocotyle umbellata</i> or <i>verticillata</i>	Apiaceae	16	108	M**
Wand Goldenrod	<i>Solidago stricta</i>	Asteraceae	36	81	M**
Basketgrass	<i>Oplismenus hirtellus</i>	Poaceae	19	92	M**
Carolina Wild Petunia	<i>Ruellia caroliniensis</i>	Acanthaceae	15	59	M**
Sawgrass	<i>Cladium jamaicense</i>	Cyperaceae	22	33	
Straw-colored Flatsedge	<i>Cyperus</i> cf. <i>strigosus</i>	Cyperaceae	18	36	M
Erect Centella	<i>Centella erecta</i>	Araliaceae	1	48	M
Frogfruit	<i>Phyla nodiflora</i>	Verbenaceae	4	37	M**
	<i>Dichantherium</i> sp.	Poaceae	13	26	M
unidentified grass*		Poaceae	9	26	M
Trumpet Creeper	<i>Campsis radicans</i>	Bignoniaceae	3	32	M**
black/dewberry	<i>Rubus</i> sp.	Rosaceae	1	33	M**
rosette grass	<i>Dichantherium</i> sp.	Poaceae	10	21	M
	<i>Mikana</i> sp.	Asteraceae	7	20	M
Shiny Woodoats	<i>Chasmanthium nitidum</i>	Poaceae	7	19	M
unidentified herb*			4	22	M**
Saltbush	<i>Baccharis halimifolia</i>	Asteraceae	7	17	M
Saltmarsh Fingergrass	<i>Eustachys glauca</i>	Poaceae	10	13	
Florida Paspalum	<i>Paspalum floridanum</i>	Poaceae	7	14	
Rice Button Aster	<i>Aster dumosus</i>	Asteraceae	1	20	M**
unidentified legume*		Fabaceae	0	21	M**
vetch	<i>Vicia</i> sp.	Fabaceae	17	4	I
White-topped Sedge	<i>Dichromena colorata</i>	Cyperaceae	0	20	M**
Giant Ironweed	<i>Vernonia gigantea</i>	Asteraceae	9	10	
Climbing Aster	<i>Symphotrichum carolinianum</i>	Asteraceae	1	17	M**
Saltmarsh Morning-glory	cf. <i>Ipomoea sagittata</i>	Convolvulaceae	12	5	
Walter's Groundcherry	<i>Physalis walteri</i>	Solanaceae	9	5	
Seaside Brookweed	<i>Samolus valerandi parviflorus</i>	Samolaceae	4	8	
jessamine	<i>Gelsemium</i> sp.	Gelsemiaceae	0	12	M**
Leafy Marsh-pink	<i>Sabatia calycina</i>	Gentianaceae	0	11	M**
unidentified herb*			0	8	M
violet	<i>Viola</i> sp.	Violaceae	0	8	M
Virginia Creeper	<i>Parthenocissus quinquefolia</i>	Vitaceae	0	8	M
unidentified herb*			0	7	M
unidentified grass*		Poaceae	2	5	
Spanish Dagger	<i>Yucca aloifolia</i>	Asparagaceae	5	0	I
Lizard's Tail	<i>Saururus cernuus</i>	Saururaceae	0	4	M
hibiscus	<i>Hibiscus</i> sp.	Malvaceae	0	4	M
Black Needlerush	<i>Juncus roemerianus</i>	Juncaceae	3	1	
unidentified herb*			1	2	
unidentified herb*			1	1	
Roundleaf Bluet	<i>Houstonia procumbens</i>	Rubiaceae	1	1	
waterhyssop	<i>Bacopa</i> sp.	Veronicaceae	0	2	
Ponysfoot	<i>Dichondra</i> sp.	Convolvulaceae	1	1	
Blue-flag	<i>Iris versicolor</i>	Iridaceae	0	1	
Jewelweed	<i>Impatiens capensis</i>	Balsaminaceae	0	1	
unidentified herb*			1	0	
bedstraw	<i>Galium</i> sp.	Rubiaceae	0	1	

Table 3-1 Continued

Common name	Latin name	Family	Occurrence (225 max)		
			Island	Mainland	More?
thistle		Cynareae	0	1	
unidentified herb*		Asteraceae	0	1	
unidentified herb*			0	1	

\*Unidentified plants were unable to be identified by the University of Florida Herbarium because the samples were either vegetative or unavailable in the case of species with a single occurrence.

\*\* The difference is still significant when a Šidák's correction for multiple comparisons is applied.

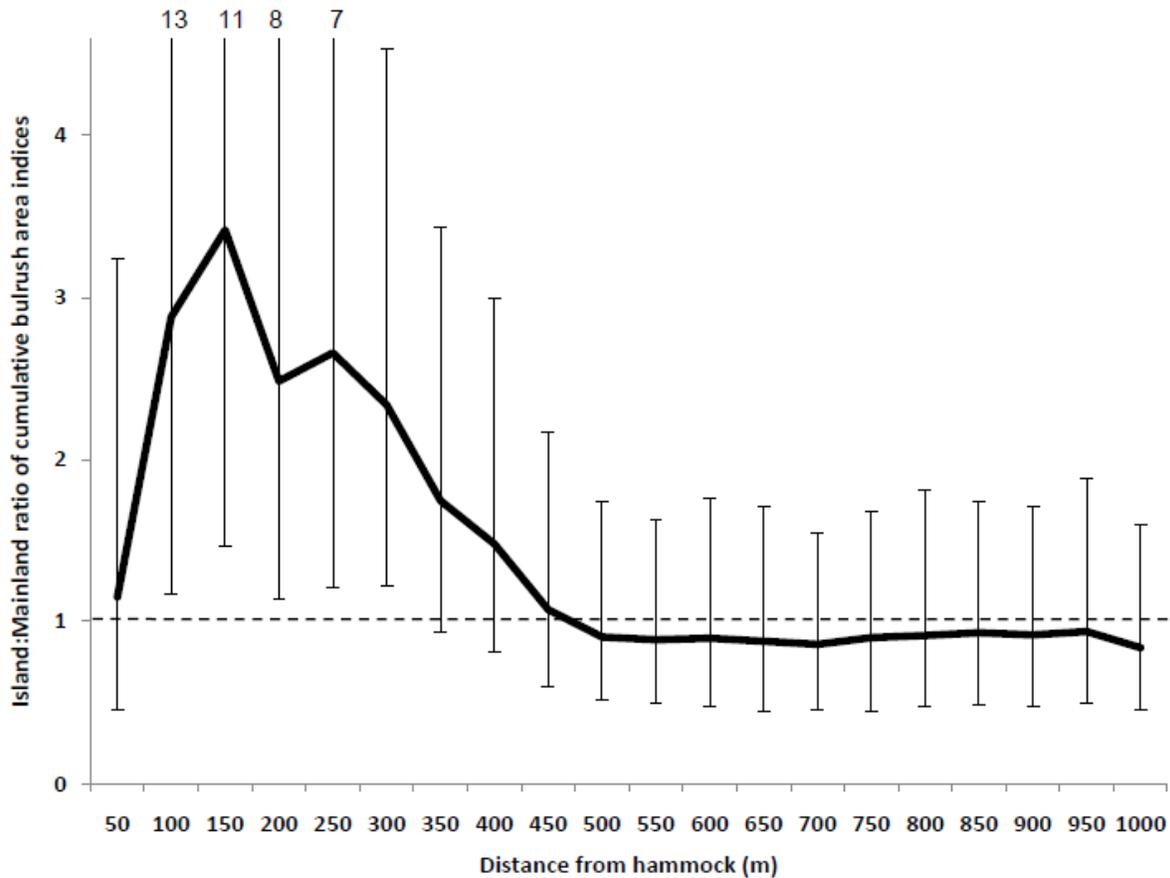


Figure 3-8. The ratio of the island and mainland cumulative bulrush area indices. Bars indicate 95% confidence intervals. Numbers above bars indicate upper 97.5% confidence limits too high for the vertical axis. Within 300 m islands are surrounded by greater areas of bulrush used as feeding grounds by the Feral Hogs than is the mainland. The highest peak (3.6) approximates and the confidence intervals between 100 and 300 m enclose the estimate for the ratio between island and mainland hog densities. At greater distances, the difference disappears and the ratio approximates 1.

Table 3-2. A comparison of Feral Hog relative abundance indices for the island coastal hammock and marsh area compared with the mainland coastal hammock area. All indices show significantly lower hog densities on the mainland. The bias towards the mainland in the three opportunistic sample-based indices results from the mainland being used to access the islands.

Index	Observations			Bias	Sampling strategy
	Island	Mainland	Island/Mainland		
Heard/Seen	90	52	1.7	Mainland	Opportunistic
Remains	23	9	2.6	Mainland	Opportunistic
Scat	1134	189	4.4*	None	Systematic
Nests	29	6	4.8	Mainland	Opportunistic

\*Corrected for sampling area.

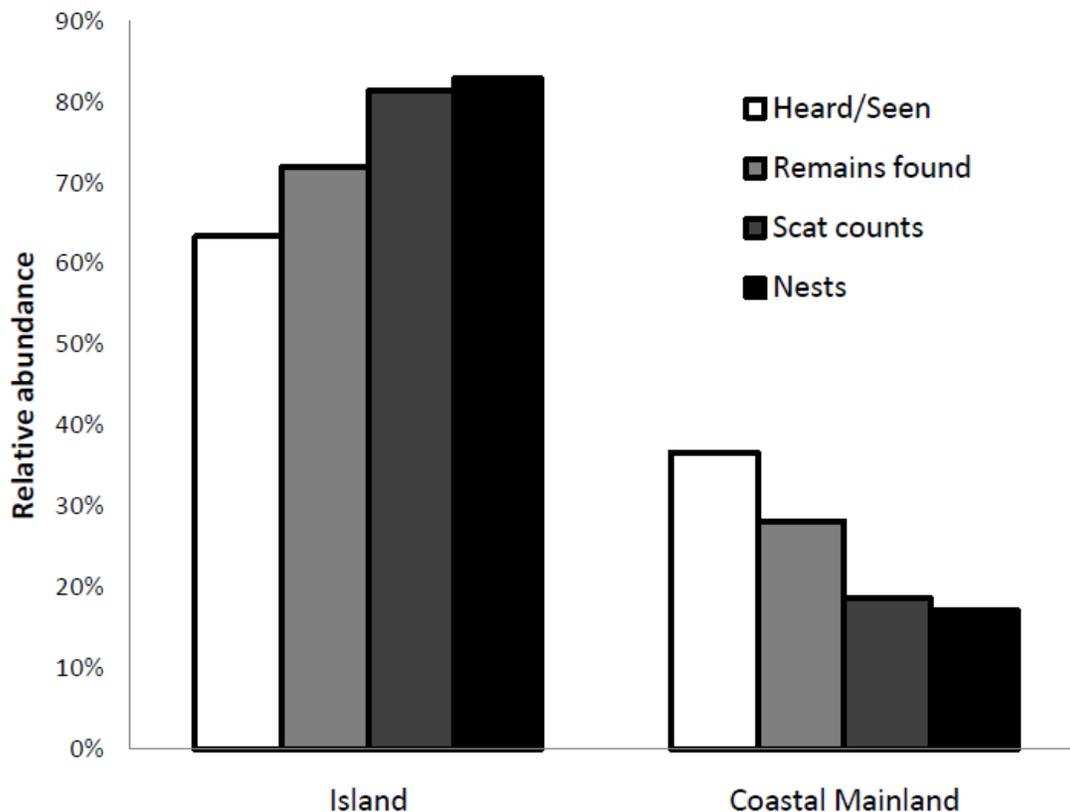


Figure 3-9. Relative abundance indices for Feral Hogs in the coastal mainland hammock and the isolated hammock islands in the marsh in the Lower Suwannee National Wildlife Refuge, Florida. The scat count index is the only one for which time spent or area covered is controlled for and is therefore unbiased. The others are probably slightly biased towards the mainland. All indices show significantly higher hog densities in the island/marsh area than on the mainland.

## Discussion

The impact of mobile, generalist consumers upon local communities of their resources is likely to reflect processes operating over broader spatial scales (Polis et al. 1997). Understanding such impacts can be crucial for a wide range of issues in conservation biology and environmental management. In our study, landscape context appeared to have a strong influence on the impact of Feral Hogs, however not always in the ways initially predicted. We first discuss the factors that control differences between hog numbers on islands and the mainland, and the seemingly contrary patterns in rooting magnitude, then turn to differences in impacts of hogs on herbaceous plant communities as revealed by the exclosure studies.

### **Island vs. Mainland Hog Numbers**

Hog density as estimated by several indices was 3-4 times higher on the island hammocks than on the mainland, reflecting, we suggest, the fact that the islands are embedded within an important feeding habitat. It is worth discussing in more detail several processes that would be operating to produce this density effect.

The hogs seem to spend a great deal of time foraging in the bulrush areas of the marsh, as judged by the extent of damage they cause there, by the cumulative impression of incidental observations, and by unpublished dietary data. Though peninsulas from the mainland do abut and extend into the marsh, an animal living on one of the islands would on average have much more access to greater areas of marsh than an animal living on the mainland (seen in Figure 3-3). Although hogs are often observed foraging in the marsh completely exposed to the sun on cloudless and hot days, hammock areas do provide shelter from the sun as well as dry land for rest and respite from flooding in the marsh and are therefore likely to be heavily used for shelter

even if lacking in food resources. Wallows are most commonly found in the shaded edges between hammock and marsh (although they do also occur at times in the marsh itself; CW, pers. obs.), which suggests that the marsh is used primarily for feeding, while the hammocks are preferred at other times for other activities.

This landscape complementation/supplementation we suggest is likely the main reason why hog densities are so much higher in the islands. This pattern is consistent with a “spill-over” effect in which smaller areas of “barren” habitat (the food-poor hammock) have much greater densities of consumers sustained in effect by more productive habitats (the feeding areas in the marsh) than would be found on greater areas of “barren” habitat (the mainland) (Oksanen 1990). Yet note that the heavy use of the islands is likely to also be related to distinct conditions they provide (viz., shade and dry land) not found in the tidal marsh and therefore this kind of landscape effect is more complex than just a simple spill-over effect.

However, other mechanisms could also contribute to the observed island effect. Another reason for the greatly elevated abundance of pigs on islands could be that the islands provide better security for piglets from mesopredators. It should be noted that Bobcats have been tracked onto the islands, as have Coyotes (whose scat has been observed to contain hog hair and small hooves, consistent with predation on piglets); mesopredators thus are unlikely to be excluded from the islands entirely. However, the islands are small and completely surrounded by periodically flooded marsh, so predator density may be lower and the ability to detect predators may be higher. In any case, hogs do not make up a large part of the diets of Bobcats and Coyotes; Florida Panthers, currently extirpated from the area, are the only effective adult hog predators that exist

anywhere in Florida (Maehr 1997). It should be noted that hunting is practiced in the refuge so human hunters are in effect another top predator on adult hogs. Many hunters know that the islands have high hog densities and so specifically hunt on the islands (C.W., pers. obs.) but hunting season is restricted to the fall/winter months. The overall combined predation risk, experienced mostly by piglets, may thus be slightly lower on the islands at least outside of hunting season.

Although this is plausible, other lines of evidence suggest that hog abundance is actually regulated by resources, rather than predation. Judging from the emaciated hogs (especially lactating females) observed during the course of this study (C.W.), top-down control (predation) is likely to be much less important than bottom-up control (nutritional stress) in determining hog density.

The area of bulrush feeding grounds surrounding the islands can be up to 3.4 times the area surrounding the mainland. The maximum access to resources conferred by island living is found by foraging within 150 meters of islands with a significant advantage extending to foraging within 300 m. Because the average distance between islands is 55 m—with even the longest nearest-neighbor distance between islands being shorter than 300 m—it is clearly more efficient to feed in bulrush areas by moving between islands rather than foraging from a mainland base; a neighborhood effect (Dunning et al. 1992). The fact that the islands appear to have similar magnitudes of higher foraging area and hog densities compared the mainland supports the conclusion that the islands are far more important for providing access to resources than they are for providing protection for predators.

This difference in consumer abundance, however, is not necessarily matched by corresponding hog impacts either as disturbance agent gauged by rooting activity or by net effects on plant communities.

### **Rooting Activity**

When there was a difference in observed rooting extent, the mainland had more evidence of rooting, despite by all signs having fewer hogs per unit area. This suggests that there is a difference in individual hog foraging behavior, depending on whether or not the hog is on an island or on the mainland. The percents of the hammock areas on the mainland rooted in 2005 (3-9%) straddle estimates made in other systems (8%, Baron 1982; 7.4%, Kotanen 1995; 4%, Mitchell & Mayer 1997; 3%, Welander 2000; 3.8%, Engeman et al. 2003). However, the level of rooting in 2006 ( $\leq 0.44\%$ ) fell far below estimates in these other systems. It must be kept in mind that this rooting estimate is limited to the hammock areas and that rooting activity in the marsh is not included. However, the area of rooting in the marsh (i.e., the bulrush areas) can be as high as 18% in the landward portion (Figure 3-3), similar to the reported 19% rooted in a Florida freshwater marsh (Engeman et al. 2004) and the marsh likely strongly supplements if not overshadows the food resources available in the hammock. The islands appear to be used less as feeding areas, even during the times the hammock habitat is heavily rooted. Instead, the islands seem to serve more as staging areas for access to more profitable marsh feeding areas.

The greater extent of rooting on the mainland than on the islands could have been due to greater herbaceous biomass there, providing more plant and possibly correlated invertebrate resources available on the mainland than found on the islands. However, this difference was not consistent through time and rooting activity on the mainland

almost disappeared in 2006. Given the notorious behavioral flexibility of Feral Hogs (Graves 1984; Oliver & Brisbin 1993), intense rooting on the mainland should be seen as an opportunistic feeding strategy either because the mainland only periodically provides worthwhile amounts of food or because it provides an important fallback feeding area when normal marsh resources fail.

One result that we did not anticipate was that tilling appeared to foster further rooting by pigs. The observation that tilling increased the chances of a plot being subsequently rooted raises some interesting possibilities. First, tilling could simply break up the soil and thus make a softer and more attractive rooting substrate for the hogs. Second, tilling could be exposing food and making its detection by hogs more likely, encouraging them to root and feed in an area. Third, tilling could initiate an information cascade by being interpreted by the hogs as evidence of other hogs rooting and finding food in an area, encouraging still more rooting of the same area. These possibilities are not mutually exclusive. Although the second possibility depends on the artifact of food remaining in a tilled area (there would presumably be less food after real rooting), the positive feedback of hogs being attracted to previously rooted areas could have a strong influence on the spatial pattern of hog damage across a landscape, increasing its spatial variance and the spatial variability of effects on the communities. This positive feeding feedback may also be at the root of the bulrush-dominated areas in the marsh that seem to be important foraging areas for the hogs. The impact of hogs specifically as ecological engineers would be an interesting focus for further study.

### **Hog Effects on Herbaceous Communities**

In spite of the fact that there appear to be much greater hog densities in the island than mainland hammocks, effects of excluding the hogs on herbaceous species

richness and cover were only seen on the mainland with island plots showing no increase in either assay of plant community structure. The decreases in species richness and cover due to the presence of hogs and increased tilling observed in the mainland areas were consistent with the known substantial impacts of hogs on herbaceous vegetation in other habitat types around the globe (Bratton 1975; Cuevas et al. 2010; Hone 2002; Kotanen 1995; Nogueira-Filho et al. 2009) as was the rapid recovery of species richness after tilling was ceased (Kotanen 1995). However, the lack of effect of exclosures and tilling on herbaceous species richness and cover on the islands was completely unexpected.

We suggest the following scenario as a plausible explanation for this effect. This scenario involves the confluence of several factors, some reflecting the likely nature of hog responses to habitat spatial heterogeneity, and some to differences between island and mainland plant communities in this environment.

Even though hog densities appear to be 3 to 4 times higher on the islands, it was the mainland herbaceous community that responded to the exclusion of hogs. This seems consistent with the observation that rooting itself was more intense on the mainland at the beginning of the study, however the response to hog exclusion occurred within a year, thus the impacts of higher hog rooting on the mainland early in the study would have disappeared in the control plots as the reduction in mainland rooting occurred long before the end of the study. Thus the final effect of the exclosures would have been zero if it had been only the impact of hog rooting that was being excluded. Additionally, tilling had an effect on the mainland but not on the islands, the opposite of

what would be expected if the initial higher levels of rooting on the mainland were driving the treatment effect of the exclosures on the herbaceous community.

The unresponsiveness of the island herbaceous community arguably reflects how pigs, which have been present in this ecosystem for centuries, can act as environmental filters for plant communities. If one is to observe an increase in species richness in a prey community after a predator or other consumer is removed, then species which are being strongly impacted must still be present in low numbers or sufficiently close in space to provide dispersing propagules. If hogs differentially and strongly affect certain species, sustained higher hog densities on islands may have simply extirpated long ago disturbance-vulnerable plants, thus precluding the observation of an effect of hog removal on island plant communities, at least over the time-scale of this study. There are many examples in other systems of generalist predators eliminating vulnerable prey species from small islands (Holt 2010). The islands in the study are obviously smaller in area than the mainland habitat, and so a given intensity of suppression via any means (as measured say in a fractional reduction in a species' abundance) will lead to lower total population sizes for affected species, and thus higher likely extinction rates. The fact that the island community is essentially a subset of the mainland community and most species occurred with greater frequency on the mainland support this thought. Moreover, the spatial patchiness of hog disturbance means that in larger mainland areas, some plants may escape destruction by chance and provide foci for re-colonization. The islands are less likely to harbor such refuges simply because of their constricted size. Thus, hog-vulnerable species could potentially have populations on the mainland because either the land area is large enough to support stable populations

at low densities overall or there are permanent refuge areas of lower disturbance, or because areas lie undisturbed long enough as transient refuges for vulnerable plants to colonize, grow, reproduce, and colonize new patches before hogs use the area again.

While the exclosures on the mainland could have been colonized by hog-vulnerable plants that were able to survive either in low densities or in spatial or temporal refuges, the islands are too small for any of these mechanisms to function and thus we suggest all the vulnerable plants in the regional species pool were likely to have been extirpated from the islands long ago. The observation that the remaining island community was more resistant to impacts of Feral Hogs is consistent with Baron's (1982) study that showed that Feral Hogs had no effect on the flora of an island that constantly experienced disturbance (in that case from inclement weather). However, in the current study, the mainland areas and the islands are extremely close and likely experience similar overall climatic-physical disturbance regimes but the much higher densities of hogs on the islands increase biotic disturbance rates. Thus the hogs appear to have produced a disturbance-resistant herbaceous community on the islands by restricting the species in the regional pool that are able to survive there.

This idea is also supported by the results on herbaceous cover. Hog exclusion may have slightly increased the herbaceous cover in the mainland, but it had no impact on the islands. Tilling did have an effect in both areas, but it was much greater on the mainland. Thus not only were the species richnesses of the islands affected less by both treatments, but the cover of the entire community was less impacted by the treatments on the islands. These results again imply that the subset of herbaceous

species found on the islands is there largely because it is composed of plant species that survive disturbance by Feral Hogs.

Oddly, however, exclusion of hogs had a positive effect of similar magnitude on the herbaceous biomass on both the islands and the mainland. This result shows that the hogs are having an impact on the herbaceous community viewed in aggregate. This result is not in contrast with the species richness and cover results, which suggest that the species found on the islands are the species better able to deal with the impacts of Feral Hogs.

The marsh likely forms a barrier to dispersal for many plants making the island communities more dispersal-limited than communities on areas of similar sizes on the mainland. Wind-dispersed seeds that manage to escape a sheltered hammock environment and travel through the marsh are more likely to be stopped by the longer edge of the larger mainland hammock. Seeds dispersed by gravity or autochory are very unlikely to make it across the marsh barrier at all, as are seeds dispersed by small mammals. However, seed dispersal by birds or large mammals (especially by hogs) is unlikely to find the marsh a firm barrier. The fact that the hog exclosures were 4 m x 4 m makes them essentially very small targets and therefore unlikely destinations for rare propagules. So over the course of this study, long-distance colonization (*e.g.*, from mainland sources) seems exceedingly unlikely.

This study demonstrates the importance that landscape patterns can have in determining the impact of a consumer with little top-down control. In this case, the mechanisms involved appear to be landscape complementation and a neighborhood effect, in which the spatial juxtaposition of distinct required resources alters the effective

density and movement of the actor and therefore its impacts on the system, and an emergent island effect, in which isolated and small local communities are vulnerable to species loss and have fewer opportunities for recolonization. Both of these mechanisms can be useful for prioritizing conservation responses to exotic species like Feral Hogs.

Controlling Feral Hog populations often proves difficult (Cowled et al. 2006; Cruz et al. 2005; Hampton et al. 2004b; McIlroy & Gifford 1997) and is more likely to be economical and effective if their vital resources are understood and incorporated. For example, Feral Hogs are tied to water so moist areas not only have the highest densities of hogs (Adkins & Harveson 2007; Baber & Coblenz 1986), but in dry areas each waterway may have a relatively independent population making it more effective to concentrate elimination efforts on a single waterway at a time rather than in multiple areas simultaneously (Hampton et al. 2004b). In the coastal hammock system, access to marsh resources appears to be important in maintaining high densities of hogs, so control efforts focusing on the marsh are likely to be more effective at reducing the hog population than would be diffusing efforts over a wider area.

In addition to providing guideline strategies for more effective control of exotic species, an understanding of landscape patterns and how they influence the impacts of the exotic may be able to help focus efforts to conserve endangered native species by indicating which areas are most likely to be heavily impacted and, furthermore, which species in those areas are especially likely to be vulnerable (Jolley et al. 2010). This is especially the case in recently invaded areas where impacts on the ecosystem are at an

early stage and species numbers and population levels have not yet been fully altered by the exotic species.

The hogs have a clear top-down impact on the herbaceous community of the hammock. Not only do they reduce the plant biomass on both the island and the mainland areas, they also were shown to have more complex interactions in that they reduced the species richness and cover in only the mainland hammock. They are likely to have had even greater impacts on the islands that are too long-term to have been detected by this study. Testing this idea might require either much longer term or larger exclosures or directed colonization of species present on the mainland but absent on the islands. The lack of effective predation on the adults probably allows for much greater densities and impacts of hogs than would be seen if the only effective predator of hogs in Florida, the Florida Panther (Maehr 1997), were still in the area. The dominance of Feral Hog in the diet of the Florida Panther, the high densities of hogs across much of Florida, and the importance of top-down impacts in this community suggest an avenue through which the extirpation of a top predator is having continued influence on community characteristics.

## CHAPTER 4 ALTERATION OF NUTRIENT FLOWS BY AN EXOTIC SPECIES

### **Introduction**

Patterns of nutrient and energy flow within ecosystems have long been considered to be central to ecology and the functioning of ecosystems (Evans 1956). The importance of animal-mediated nutrient flows between different ecosystems and habitats is becoming increasingly recognized in many different contexts (Polis et al. 1997, Vanni et al. 2004). These nutrient flows can be disrupted by population reductions and extinctions of some nutrient transporters (Sekergioglu 2006) or by the increase in importance of others, including exotic species. Changes in patterns of nutrient flow can alter competitive interactions within communities (Keddy et al. 2000), vulnerability to exotics (Thompson & Leishman 2005), and even the physical structure of communities (Croll et al. 2005) making conservation more challenging. These changes may be further exacerbated by anthropogenic habitat reduction, degradation, and fragmentation and the introduction of exotic species.

Human actions often benefit medium- and small-sized mammalian generalists (DeStefano & DeGraaf 2003, Fraterrigo & Wiens 2005, Prange et al. 2004, see Chapter 2) due to declines in large predators (Gipson 1978), reductions in specialist competitors (Foufopoulos & Ives 1999, Henle et al. 2004), increases in landscape diversity (Marzluff & Neatherlin 2006), appearances of novel resources (Marzluff & Neatherlin 2006), and introductions to new areas (Ruesink 2005). All these changes typify human-landscape interactions. Because generalists tend to increase in human-impacted landscapes, their importance to nutrient flows is probably increasing. This could amplify nutrient ties

between systems as generalist omnivores can use multiple habitat types for different resources.

In many anthropogenic landscapes, the existence of refuges is needed for continued survival of larger vertebrates (Livingston et al. 2002). Refuges serve as areas to avoid persecution or disturbance, breeding habitat, or simply provide space for den sites (Tigas et al. 2002). Because foraging may involve ranging to different habitats when resources are found concentrated in non-refuge areas (agricultural lands, middens, *etc.*), nutrients sequestered from feeding habitats are likely to be concentrated in refuges.

Nutrient transport can be important over both large and small distances (Durbin et al. 1979), for instance, when the nutrients are retrieved from a sink (Vanni & Headworth 2004) or transported from resource-rich zones (Johnston & Naiman 1987), which are characteristic of human-impacted areas (Prange et al. 2004). However, most previous work has focused on stable, usually natural, conditions (Vanni et al. 2004) or on the extinction of an important nutrient transporter (Croll et al. 2005). Examinations of nutrient flow patterns under conditions of species additions or increases are sparse. Because global anthropogenic changes favor generalist omnivores, their roles in mediating nutrient flow patterns need to be explored (Chapter 2).

In this study, the nutrient transport function of a globally important generalist omnivore, Feral Hogs (Oliver & Brisbin 1993), is examined in a system that has been shaped by human activities largely through the introduction of exotics (specifically hogs) and the elimination of effective predators (Maehr 1997). This system, the coastal marsh/hammock complex in Florida, is an intermingling of refuge areas for hogs (the

hammocks) and feeding areas (the marsh) (Chapter 3). This provides an opportunity to examine how Feral Hogs shape the nutrient regime of a complex landscape.

Feral Hogs make excellent subjects for a study of nutrient transfer on a landscape level because of their relatively large size, omnivorous diet, high population densities, flexible foraging strategies (Mayer & Brisbin 1991), and high fecundity and growth rates (Oliver & Brisbin 1993). The effects of feral pigs have been studied in many different ecosystems in numerous countries (Anderson & Stone 1993; Baron 1982; Cruz et al. 2005; Engeman et al. 2003; Ilse & Hellgren 1995; Kotanen 1995; McIlroy & Gifford 1997; Singer et al. 1984). However, most studies on environmental impacts of pigs have been limited to measuring rooting damage, erosion, and the direct effects of feeding and other activities on native communities (*e.g.*, Bratton 1975; Ickes et al. 2001), while very few examine their impact on ecosystem attributes such as nutrient regimes (but see Mohr et al. 2005). I here use Feral Hogs as a model organism to investigate the characteristics and extent of nutrient flow mediated by a generalist omnivore in a human-altered system.

I hypothesized that a source of the hog-transported nutrients is found in the marsh and that inter-habitat nutrient transfer will be unbalanced, with a net flow of nutrients into refuge areas. First, the source of the nutrients will be established through fecal dietary analysis and verified through stable isotope analysis. Then, the relative nutrient deposition in different refuge areas will be estimated through fecal count surveys and estimates of absolute nutrient deposition rates will be made based on fecal nutrient analysis and estimated fecal production rates of Feral Hog populations. The impact of nutrients transported to the refuge areas will be examined through soil and plant tissue

nutrient levels inside and outside of hog exclosures. Finally, the potential importance of long distance transport in this system will be examined through the use of stable isotopes and genetic techniques to explore population structure and size and the potential for movement of individuals between the coast and interior.

## Methods

### Study site

The Lower Suwannee National Wildlife Refuge (LSNWR; 214 km<sup>2</sup>) is on the west coast of Florida (29° 17' N, 83° 10' W) and is centered on the mouth of the Suwannee River. Inland, the habitat is composed primarily of planted upland pine woodlands and secondary growth lowland hardwood swamps. The study site is located in a portion of the refuge south of the river on the coast (Figure 4-1). The coastline is rimmed by tidal marsh, a slightly brackish marsh (1-2 ppt, unpub. data) fed by the Suwannee River and California Swamp. The marsh is dominated by the fresh/brackish water Saw-grass (*Cladium jamaicense*) and Black Needle Rush (*Juncus roemerianus*). A somewhat salt-tolerant species, *J. roemerianus*, extends more seaward than *C. jamaicense*, which lines creeks and hugs the coastal hammocks. The American Bulrush (*Schoenoplectus (Scirpus) americanus*) is found in areas that are less densely vegetated and have a disturbed looser substrate. At the complex boundary between the coastal hammock and the marsh, these three species form a mosaic of patches dominated by a single species. There are also a few small (~ 10 m<sup>2</sup>) evaporation pools bordering coastal hammocks that are dominated by Spike Grass (*Distichlis spicata*).

The coastal hammock bordering the tidal marsh is characterized by Eastern Red Cedar (*Juniperus virginiana*) and Cabbage Palm (*Sabal palmetto*), with oaks (*Quercus* sp.) and planted native pines (*Pinus* spp.) also being common. The subcanopy is

dominated by Yaupon Holly (*Ilex vomitoria*), bay (*Persea* spp.) and, in the drier areas, Saw Palmetto (*Serenoa repens*). In addition to the mainland, the coastal hammock is found on small (~1000-12,000 m<sup>2</sup>) forested islands embedded in the tidal marsh. The amount of herbaceous undergrowth varies greatly from essentially none in the wettest areas to high cover in the areas least subjected to flooding.

Feral Hogs are a conspicuous element in the local mammal community. The Nine-banded Armadillo (*Dasypus novemcinctus*), Virginia Opossum (*Didelphis virginiana*), and Raccoon (*Procyon lotor*) are common in the coastal hammock including the islands. Less common are the Coyote (*Canis latrans*) and Bobcat (*Felis rufus*), the latter of which travels through the marsh to the coastal hammock islands. White-tailed Deer (*Odocoileus virginianus*) are rare but present throughout the coastal hammock including the islands. Feral Hogs (*Sus scrofa*), however, are extremely common (pers. obs.; Mayer & Brisbin, 1991).

The sampling area of the study contained of three coastal hammock areas of the mainland and 8-10 islands on either side of Barnett Creek. All of these areas were within 1.25 km of each other (Figure 4-1).

## **Study Design**

### **Fecal/tissue samples**

Fresh (< 1 week old, usually < 3 days old) hog fecal samples were gathered either opportunistically throughout the study or specifically sought by intensively searching areas with fresh hog sign or by stalking and backtracking observed animals. Fecal samples were stored in 95% ethanol at -40° C. Each sample consisted of a single fecal 'pile' (as defined below). Tissue samples were gathered opportunistically from hunters

or road killed animals and stored at  $-40^{\circ}$  C. Fecal samples were used to for dietary, nutrient, and genetic information (below).

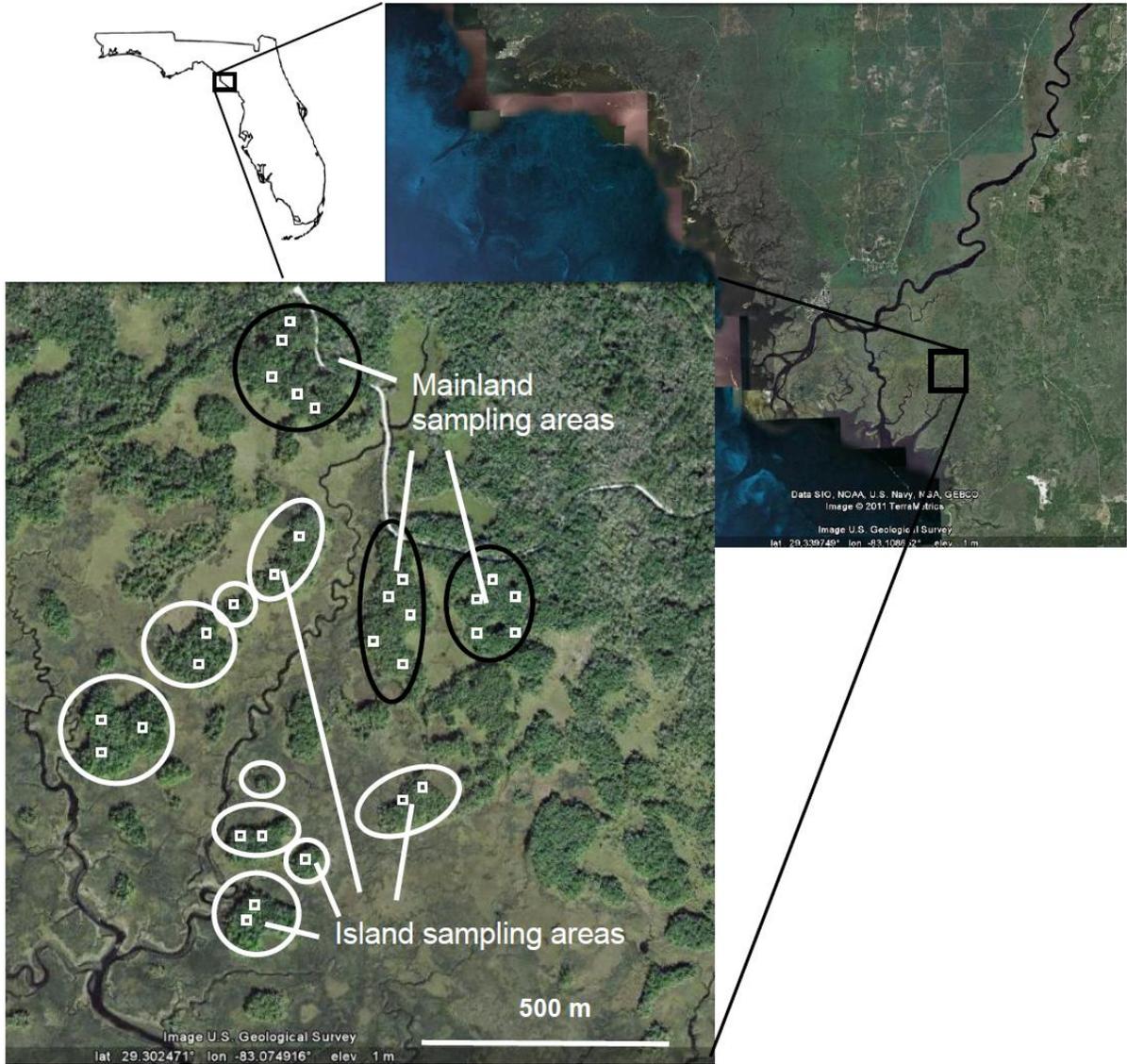


Figure 4-1. An overview of the study site in the Lower Suwannee National Wildlife Refuge, Florida. Coastal hammock “mainland” and “island” sampling locations for this study are indicated. Locations of plot sets are indicated by squares.

## Diet

**Fecal dietary analysis:** Fecal samples were washed over a 2 mm sieve and the retained material identified under a dissecting microscope. If necessary, identification was assisted by comparison with ground or whole specimens from known food species. Each sample was systematically examined and all components recorded. Percent composition was estimated with a point-sampling method by spreading the samples evenly over a 5 x 5 grid of points and recording the material over each point. If more than one component occurred over the same point, the score for that point was divided between them. Categories were added as needed. 'Detritus' was defined as vegetation that appeared to have been dead when consumed and was likely ingested incidentally during feeding. Examples included pine and juniper needles, oak leaves, palm wood, palm leaves, and twigs. A food was considered to have been intentionally consumed if the amount in a sample exceeded the maximum amount of detritus found in all the samples. Unmasticated maggots, dung beetles, and fungus were ignored as obvious post-excretion additions. The only fraction that proved impossible to identify was masses of white slimy mucus in one specimen.

**Stable isotopes:** Bone samples of hogs and other omnivores (Virginia Opossum, *Didelphis virginiana*; Raccoon, *Procyon lotor*; Marsh Rice Rat, *Oryzomys palustris*; and Hispid Cotton Rat, *Sigmodon hispidus*), strict herbivores (White-tailed Deer, *Odocoileus virginianus*, and Domestic Cattle, *Bos primigenius taurus*) and carnivores (American Alligator, *Alligator mississippiensis*, and River Otter, *Lontra canadensis*) were gathered opportunistically during the study to clarify the trophic position of hogs in the coastal food web (Minagawa et al. 2005) using isotopic analysis. Though no cattle are currently found in the LSNWR, they were previously run in the area and bone specimens of

young animals were infrequently found. Hog skeletal remains were common. However other species proved to be rare, and sample sizes are therefore limited. For comparison with coastal hogs, samples of inland hogs were also opportunistically gathered or were taken from museum specimens kept in the Florida Museum of Natural History (catalogue numbers UF2048, UF3282, and UF5975).

The two fractions of bone typically used in stable isotope analyses are the mineral fraction, apatite, and the protein fraction, collagen. The collagen fraction contains both nitrogen and carbon. Stable isotope values are reported in the  $\delta$  notation ( $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$ ). For example,  $\delta^{15}\text{N}_{\text{sample}} = (((^{15}\text{N}/^{14}\text{N})_{\text{sample}} / (^{15}\text{N}/^{14}\text{N})_{\text{standard}}) - 1) \times 1000$ , and thus the units are per mil (‰). The standard for nitrogen is atmospheric nitrogen. The standard for carbon is Peedee Belemite limestone (Kelley 2000). The nitrogen reflects the protein in the diet that is retained and incorporated into body proteins. However, as some dietary proteins are burned for energy and this process selectively metabolizes the lighter isotopes, the nitrogen signal of the collagen is enriched in the heavier isotopes compared to the signal of the diet (this is generally 2-5‰; hog-specific fractionation is discussed below) (Ambrose et al. 2003).

The collagen carbon is largely derived from the carbon in the protein source, both because essential amino acids by definition retain their original composition and because it is more metabolically efficient to use non-essential amino acids from the diet when possible (Ambrose et al. 2003). As discussed below, fractionation of carbon between trophic levels is relatively small but there is fractionation among different tissue types of the same individual that must be accounted for.

The apatite fraction contains carbon-containing carbonate derived from carbonic acid in the blood. This carbonic acid is in turn derived from metabolizing organic molecules to release energy and CO<sub>2</sub>, which dissolves in the blood forming the carbonic acid. Thus the carbon signal of the apatite fraction of the bone reflects foods that are metabolized for energy. In an omnivore, carbohydrates are often the main energy source but amino acids that are not incorporated into proteinaceous tissues are also metabolized for energy. Therefore, the carbon signals in collagen and apatite often tell different stories with the collagen signal reflecting protein sources in the diet (meat) and the apatite signal reflecting the whole diet (Ambrose et al. 2003). The differences between the two signals should be the greatest in individuals who have moderate amounts of meat in their diet and the differences should be less when individuals have very little (so are getting most of their protein from the same plant foods as their carbohydrates) or an over abundance of meat (so are burning a great deal of protein as energy).

Collagen and apatite fractions of the bone samples were isolated with standard techniques (Ambrose 1993) in the Bone Chemistry Laboratory in the University of Florida Department of Anthropology. Bone samples were scraped clean of visible dirt and sonicated in deionized distilled water (DI-H<sub>2</sub>O) in 10 minute treatments until the water was no longer cloudy. Lipids were removed under pressure with Accelerated Solvent Extraction (model ASE300; 2:1 dichloromethanol:methanol; two cycles of heating for 5 min to 100°C, static for 5 min, 60% volume flushed, and purged for 100 sec), and the bone was ground into powder with a mortar and pestle or Spex mill. The

resulting powder was sieve partitioned into two size categories: particles 0.50 mm to 0.25 mm in size (for collagen) and particles < 0.25 mm in size (for apatite).

Apatite was purified from the < 0.25 mm fraction by treatment in a 2% NaOCl solution for 16 hours to oxidize the sample and remove the organic portion of the bone. The samples were then rinsed with distilled water to neutrality and treated with a 0.2 M solution of acetic acid for 16 hours (to remove any diagenic carbonates). The samples were rinsed to neutrality and lyophilized.

Collagen was purified from the 0.25 – 0.50 mm fraction by treatment in 0.2 M HCl (replaced every 18 hours) to demineralize the bone until purified collagen was visually apparent (collagen is lower density than bone and sinks slowly after agitation). The samples were then rinsed to neutrality with distilled water and treated with 0.0625 M NaOH for 16 hours. The samples were again rinsed to neutrality, placed in 10 ml of  $10^{-3}$  M HCl, and heated at 95° C for 5 hours to dissolve the collagen. To completely dissolve the collagen, 35  $\mu$ l 1 M HCl were added to the samples, which were heated at 95° C for another 5 hours. The evaporated liquid was replaced with  $10^{-3}$  M HCl. The solution was separated from the solid fraction with centrifugation and evaporated at 65° C to ~2 ml before being lyophilized.

In addition to vertebrate bones, the isotopic signatures of putative foods/basal resources were also measured. Plant samples were gathered from the marsh, the islands, the coastal hammock mainland, and from three inland locations in the refuge. The samples were sonicated in distilled water until the water no longer became cloudy. They were then dried at 50° C and ground in a Wiley mill. Invertebrate samples were removed from the shell and dried at 50° C, before being ground in a Wiley mill. Gastric

contents were retained as they would be consumed by the hogs along with the invertebrate tissue. In 7 out of 11 cases, the invertebrate samples comprised one individual. In the other cases, the samples contained more than one individual. The samples were weighted accordingly during statistical analysis. Invertebrates were divided into two groups based on diet and stable isotope signatures:

omnivores/detritivores (the Carolina Marsh Clam, *Polymesoda caroliniana*; Gulf Mud Fiddler Crab, *Uca virens*; Heavy Marsh Crab, *Sesarma reticulata*; and the Olive Nerite, *Vitta usnea* syn. *Neritina reclinata*) and herbivores (Florida Marsh Snail, *Detracia floridana*)

Stable isotopes signatures ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) were measured in the Light Stable Isotope Laboratory in the Department of Geological Sciences at the University of Florida. Plant and invertebrate samples were measured on a Finnigan-MAT 252 isotope ratio mass spectrometer with a ConFlow II interface linked to an elemental analyzer. The results were corrected against the USGS40 (L-glutamic acid) standard (n = 6) with measurement precisions of  $\pm 0.10\%$   $\delta^{13}\text{C}$  and  $\pm 0.14\%$   $\delta^{15}\text{N}$ . Two samples (a *Smilax* and a bulrush) had odd chromatograms and  $\delta^{15}\text{N}$  values were enriched by more than an order of magnitude over the other samples. These were rerun, with similar but numerically inconsistent results, so they were considered contaminated and not used.

The apatite fraction of the bone samples was measured on the Finnigan-MAT 252 with a Keil III carbonate preparation system. The results were corrected against the NBS-19 (TS limestone) standard (n = 8) with a measurement precision of  $\pm 0.017\%$ . The collagen fraction of the bone samples was measured by first determining the C:N atomic ratio of each sample with a Carlo Erba NA1500 CNS elemental analyzer and

corrected against an atropine standard (70.56% C, 4.84% N, n = 6) with measurement precisions of  $\pm 0.07\%$  N and  $\pm 0.75\%$  C. All bone collagen samples had acceptable C:N ratios (2.9-3.6) (DeNiro 1985). Stable isotope ratios were measured on the Finnigan-MAT 252 with the ConFlow II interface and corrected with the USGS40 standard (n = 9) with precisions of  $\pm 0.07\%$   $\delta^{13}\text{C}$  and  $\pm 0.11\%$   $\delta^{15}\text{N}$ .

There is little fractionation between diet and whole animal for  $\delta^{13}\text{C}$  ( $< 2\%$ ) compared to the range of  $\delta^{13}\text{C}$  values produced by differing methods of photosynthesis (average for  $\text{C}_3 = -27\%$ ;  $\text{C}_4 = -13\%$ ) (Kelly 2000). However there is a fractionation of  $^{13}\text{C}$  among the tissues within an animal. The isotopic signature of diet of the hogs was calculated by accounting for the average carbon fractionation between whole hog diets and hog apatite (average =  $10.2\%$   $\delta^{13}\text{C}$ , SD =  $1.3\%$ ; Howland et al. 2003) and the average nitrogen fractionation between hog diets and hog collagen (average =  $2.25\%$   $\delta^{15}\text{N}$ , SD =  $0.07\%$ ; Hare et al. 1991). Apatite carbon signatures were used to estimate the signature of the hog diet because the fractionation from diet to bone collagen is more variable (CV = 72.4%) than that of the apatite (CV = 12.7%) (Howland et al. 2003).

Because  $^{15}\text{N}$  is enriched with increasing trophic level, suckling young are often enriched compared to their mothers when the females are catabolizing tissues to produce milk (Newsome et al. 2006; Polischuk et al. 2001; Sare et al. 2005), although this does not occur in all species or situations (Jenkins et al. 2001). This phenomenon was examined as a contributing factor to the spread in  $\delta^{15}\text{N}$  values of the coastal hogs with a Spearman's correlation between age rank of specimens and  $\delta^{15}\text{N}$  values. Specimens that included tooth rows were assigned a relative ranking based on tooth eruption. Adults with completely erupted third molars were ranked based on tooth wear.

Interior hogs were not included in this analysis because basal resource  $\delta^{15}\text{N}$  values in different areas can vary dramatically (Ambrose 1993; Kelly 2000; Peterson & Fry 1987).

The amount of  $\text{C}_4$ -derived material in the diet of the hogs was estimated using a standard linear mixing model (Phillips & Gregg 2003) based on the  $\delta^{13}\text{C}$  signature of bulrush and the average  $\delta^{13}\text{C}$  signature of  $\text{C}_4$  plants from this study for the coastal hogs, and the average  $\delta^{13}\text{C}$  signatures of  $\text{C}_3$  and  $\text{C}_4$  plants from this study for the inland hogs. Because feeding maize to wildlife for hunting purposes appears to be common (pers. obs.), the potential contribution of maize to the hog diet was estimated in the same way, but with the  $\text{C}_4$  signature replaced by the maize  $\delta^{13}\text{C}$  signature from Hare et al. (1991), which is intermediate between and similar to values given in Norr (2004) and Howland et al. (2003).

### **Nutrient deposition**

The standing crop of Feral Hog feces in the coastal hammock was estimated by counting the number of piles of feces in 2 m x 50 m transects at the end of each season from the summer of 2005 to the spring of 2006. Feces were considered to be in a 'pile' when they were within 0.5 m of each other and appeared to be the same age and similar in size and composition. Due to the non-normal distribution of the data, the number of fecal piles for the mainland and islands were compared using a Wilcoxon sum rank for each season.

Subsamples of the hog fecal samples were sent to the Institute for Food and Agricultural Sciences Analytical Research Laboratory (IFAS-ARL) at the University of Florida for manure analysis of potassium, phosphorus, and total Kjeldahl nitrogen. For K and P, the samples were combusted at 550°C for 4 hours and the ash digested in HCl. The resulting solution was diluted with distilled water and the K and P levels

measured with an inductively coupled plasma emission spectrometer (Peters et al. 2003). For total Kjeldahl nitrogen, samples were digested overnight at room temperature in an  $\text{H}_3\text{SeO}_3/\text{H}_2\text{SO}_4$  digestion mixture and then further digested for 80 minutes at 370-400°C. The resulting solution was measured using an Alpkem colorimetric autoanalyzer (Peters et al. 2003).

Estimated fecal deposition rates were estimated by combining hog densities and body masses from similar systems (27 pigs/km<sup>2</sup>; 44.9 kg; Saunders & McLeod 1999) and solid waste production of Domestic Hogs (Chastain et al. 1999), which resulted in an estimated deposition rate of 800 ±340 SD kg of feces/km<sup>2</sup>/year (see also Appendix B). This was adjusted with the fecal count relative abundances of the mainland and islands and the measured fecal nutrient content from this study to estimate the nutrient deposition rate from feces in the different areas. Because nutrient deposition occurs through urine in addition to feces, N, P, and K deposition through urine was estimated based on calculated fecal nutrient deposition and the proportions of N, P, and K in Domestic Hog nutrient budgets excreted in the feces and in urine (Kephart & Sherritt 1990; Sands et al. 2001).

### **Soil and vegetation nutrients**

**Exclosures:** 30 sets of 4 m x 4 m plots were set up: 15 sets on the mainland and 15 on the islands. Five plot sets were placed in each of the 3 mainland areas. The number of plot sets on the islands varied from 1-3 based on the size of the islands. The plot sets were placed to maximize the diversity of the herbaceous community sampled while spacing out the plot sets as much as possible. Each set consisted of three plots: a control, an exclosure, and a tilled plot (to mimic increased hog rooting). Once the 4 m x 4 m exclosures were built with 3' hog wire fencing, the two of the four areas bordering

the sides of each enclosure that most resembled the enclosure in herbaceous community were chosen for the other two plots and randomly assigned to either till treatment or control. The external plots were given a 1 m buffer zone from the enclosure. Tilled plots were lightly tilled every six months to a depth of ~5-10 cm to mimic the physical disturbance of hog rooting. The presence of fresh hog rooting in the external plots was noted opportunistically throughout the study.

**Nutrient analysis:** Three sub-samples of soil were taken from near the center of each plot every six months (3 months offset from the tilling of the tilled plots) from summer 2007 to spring 2009 and one final time in the winter of 2010-2011. The samples were dried, sifted twice through 2 mm screen, and sent to IFAS-ARL for analysis of nitrate/nitrite, potassium, and phosphorus concentrations. These analyses were done as nitrogen, potassium, and phosphorus are important macronutrients and often limiting for plant growth. Nitrate and nitrite are the forms of nitrogen most readily available for plant uptake. Samples used for NO<sub>x</sub> analysis were water extracted as nitrate and nitrite are very water soluble. Because P and K are not as water soluble, samples for potassium and phosphorus analysis were extracted with the Merlich 1 technique, the standard for non-alkaline Florida soils (Mylavarapu & Kennelley 2002). Merlich 1 extraction uses a mixture of hydrochloric and sulfuric acids to extract soil nutrients. The nutrient concentration of the resulting solution is analyzed with spectrophotometry and, in the case of phosphorus, colorimetry (Mylavarapu & Kennelley 2002).

In the spring of 2011, plant samples were taken to estimate the nutrient content of the living aboveground biomass of the herbaceous community in the plots. For plants

with woody stems (e.g., *Smilax* spp. and *Rubus* spp.) only the leaves were taken. Poison ivy (*Rhus radicans*) was not sampled at all. Though somewhat widely spread, *Smilax* and *R. radicans* especially, these genera were always at very low density and would have added little to the overall biomass.

For plots in which the biomass was sparse, the entire aboveground living herbaceous biomass was taken. In more thickly populated plots, a subsample of the plot's biomass was taken from non-overlapping randomly placed 1 m x 1 m quadrats until the 1 liter sample bag had been filled. The samples were then dried at 50° C, ground, and sent to IFAS-ARL at the University of Florida for potassium, phosphorus, and total Kjeldahl nitrogen analyses. Potassium and phosphorus were determined by combusting the samples at 500°C followed by digestion with 6M HCl. After dilution, the nutrient concentrations were measured with an Inductively Coupled Plasma Spectrometer (Mylavarapu & Moon 2007). Total Kjeldahl nitrogen was measured by combining the samples with Kjeldahl digestion mixture (94% K<sub>2</sub>SO<sub>4</sub>, 3% CuSO<sub>4</sub>, and 3% TiO<sub>2</sub>) and H<sub>2</sub>SO<sub>4</sub>. The samples were then digested at 250°C for 1 hour followed by digesting at 365°C for 2.5-3 hours. The solutions were diluted with distilled water and the TKN was measured with an air-segmented continuous flow Alpkem colorimetric autoanalyzer (Mylavarapu & Moon 2007).

### **Population structure**

**Coat coloration:** The coloration and location of hogs observed were recorded opportunistically throughout the study. The color categories were based on the genetics of swine coloration with each category representing a distinct genotype (Fang et al. 2009; Kijas et al. 1998; Pielberg et al. 2002) and on field distinguishability. The exception was white-belted, which, although genetically distinct from white-spotted

(Kijas et al. 1998), was lumped with white-spotted due to its low frequency and the possibility of mistaking white-spotted with belted when the hog is only partially or momentarily visible. Hog sightings were put into three categories: coastal, refuge, and inland. The refuge category included hogs seen in the refuge or along the boundaries, except those seen in the coastal hammock. The inland category included hogs seen farther inland than the refuge. During statistical analysis, categories with no observations were removed and Yate's correction was applied due to small sample sizes in some categories (Yates 1934).

**Genetics:** DNA was extracted from fecal samples with a Qiagen QIAamp® DNA Stool Mini Kit and from muscle samples with a Qiagen QIAamp® DNA Tissue Mini Kit. The concentration of extracted DNA was determined with a Nanodrop ND-1000 Spectrophotometer. That hog DNA was present in the extractions was verified by amplifying an *S. scrofa*-specific mitochondrial D-loop marker (SsD; Haunshi et al. 2009) and running a gel. Because SsD was long (835 bp) compared to the microsatellites used, it was possible that the DNA from a sample had degraded into lengths shorter than SsD but still long enough to maintain the microsatellite information. Therefore, samples with relatively high concentrations of DNA (greater than ~20 µl/ml) were checked against the longest microsatellite locus if SsD could not be amplified.

Fourteen hog dinucleotide repeat microsatellite loci (Table 4-1) were amplified for each sample with successful DNA extraction. These loci are well characterized and informative in *S. scrofa* (Lowden et al. 2002; Martinez et al. 2000; Vernesi et al. 2003) and have been useful in Feral Hog population genetics in other parts of the world (Cowled et al. 2006; Hampton et al. 2004b; Spencer et al. 2005). The 3' primers for

each microsatellite also incorporated an M13 universal primer (5'-CAC-GAC-GTT-GTA-AAA-CGA-C-3') for the attachment of a fluorescent dye. Two of the 14 microsatellites were never found to work, even on the tissue samples and were therefore dropped from use during the study.

For multiplexing, microsatellites were assigned to groups of 4 or less based on non-overlapping fragment lengths. Each microsatellite in a group was assigned one of four fluorescent dyes: 6-FAM, NED, PET, and VIC, which were attached to the 3' end of the fragments with an M13 universal primer (Schuelke 2000).

PCR reactions contained 2.5 µl bovine serum albumin, 12.5 µl GoTaq® colorless Master Mix, 0.1 µl forward primer, 1 µl reverse primer, 1 µl fluorescent dye attached to M13 universal primer, and 50 ng DNA in a final volume of 25 µl. Reaction cycles consisted of 94°C for 3 min for one cycle; 95°C for 40 s, X°C for 40 s, and 72°C for 40 s for 10 cycles; 95°C for 40s, 48°C for 40 s, and 72°C for 40 s for 30 cycles; and 72°C for one cycle. "X" represents the specific temperature for each primer (Table 4-1). The second set of cycles allows the universal primer with dye to attach and replicate into the microsatellite copies. An adjustment to this format was required by the primers with a 58°C annealing temperature, which needed a 50°C annealing temperature in the second cycle to function properly.

The microsatellite PCR products from fecal samples were diluted to two different concentrations for fragment analysis: 50x and 100x. Those from tissue samples were diluted 100x and 200x. The samples were then sent to the Interdisciplinary Center for Biotechnology Research at the University of Florida where the fragment lengths were analyzed with an AdvanCE™ FS96 system. The resulting data were interpreted with

the computer program GeneMarker® and alleles based on microsatellite length were identified for each sample. Samples with fewer than 9 successfully characterized loci were excluded from further analysis.

Table 4-1. The microsatellite loci used in this study.

Name	Temp	n <sub>A</sub>	n <sub>E</sub>	H <sub>O</sub>	H <sub>E</sub>	Success	Length
S0002	63	12	7.2	0.692	0.877	26 (33)	211-246
S0005	59	11	8.3	0.636	0.922	11 (12)	238-260
S0026	55	10	4.5	0.651	0.760	27 (43)	111-123
S0068	62	-	-	-	-	0	-
S0090	55	5	3.6	0.600	0.800	5 (5)	260-267
S0155	55	6	2.8	0.556	0.655	27 (32)	166-180
S0226	55	7	2.6	0.423	0.624	26 (43)	194-225
SW122	58	-	-	-	-	0	-
SW240	58	4	2.9	0.333	0.681	12 (12)	110-136
SW632	58	9	4.2	0.667	0.775	27 (30)	163-194
SW857	58	9	2.6	0.593	0.632	27 (46)	143-173
SW911	56	6	3.6	0.444	0.734	27 (42)	172-184
SW936	58	9	4.5	1.000	0.792	27 (46)	109-131
SW951	58	8	3.2	0.704	0.700	27 (49)	137-152

Temp = annealing temperature (°C)

n<sub>A</sub> = actual number of alleles

n<sub>E</sub> = effective number of alleles

H<sub>O</sub> = observed heterozygosity

H<sub>E</sub> = unbiased estimate of heterozygosity

'Success' = the number of individuals with that locus characterized out of the 27 individuals with ≥ 9 loci (number of individuals with that locus characterized out of the original 49 successful DNA extractions)

'Length' = observed range in base pair number

The allele data were formatted, summarized, and analyzed with the application GenAlEx 6.1 (Peakall & Smouse 2006) and the program GENEPOP 4.0.10 (Raymond & Rousset 1995; Rousset 2008) and the population structure analyzed with a Markov chain Monte Carlo algorithm in the program STRUCTURE 2.3.3 (Falush et al. 2007; Hubisz et al. 2009; Pritchard et al. 2000). STRUCTURE was run with a 50,000 burn-in period followed by 1,000,000 MCMC repetitions in 10 runs per putative K (*i.e.*, the number of populations) (Cowled et al. 2006; Spencer et al. 2005). The simulations ran from K = 1 to 5 based on the possibility that the 4 general geographic areas from which samples were drawn (Barnett Creek, Trout Creek, Salt Creek, and Levy County Road

347) could be one to several distinct populations depending on (unknown) patterns of hog movement. The computer program STRUCTURE HARVESTER (Earl & vonHoldt 2011) was used to assign the most appropriate number of clusters based on  $\Delta K$  (Evanno et al. 2005).

Effective population size was estimated using the formula  $N_e = (n_E - 1)/4\mu$ ; where  $N_e$  is the effective population size,  $n_E$  is the effective number of alleles, and  $\mu$  is the mutation rate (Frankham 1996; Kimura & Crow 1964). An assumed mutation rate of  $1.0 \times 10^{-3}$  was used following Hampton et al. (2004b) who used the same loci as this study. Actual population size was estimated based on an average  $N_e/N$  ratio of 0.11 in wild populations (Frankham 1995, 1996; McKay 2007).

## **Results**

### **Diet**

Of the 19 substances identified from 39 fecal samples only 9 were considered selected foods (i.e., appeared at least once as > 12% of any sample, the maximum amount of detritus found in a single sample) (Table 4-2, Figure 4-2). The diet of the coastal hogs in the Lower Suwannee National Wildlife Refuge was surprisingly specialized—81%  $\pm$ 5% (mean  $\pm$ SE) American Bulrush rhizome based on fecal analysis. The next highest dietary fraction was Cabbage Palm fruit/seeds, but only at 4%  $\pm$ 3%.

Of the total number of fecal samples examined, 90% contained some amount of American Bulrush rhizome and 36% contained Cabbage Palm fruit/seeds. American Bulrush rhizome was the most frequently selected food and was a selected food in 90% of the samples. The next most frequently selected food, palm fruit/seeds, was a selected food in 10% of the samples (Figure 4-2).

Table 4-2. Coastal Feral Hog diet as estimated through fecal analysis.

Diet component	Common name	Scientific name	Type	% Diet
Bulrush Rhizome	American Bulrush	<i>Schoenoplectus (Scirpus) americanus</i>	S	81.1
Palm Fruit/Seed	Cabbage Palm	<i>Sabal palmetto</i>	S	4.3
Acorn	Oak	<i>Quercus</i> spp.	S	2.5
Saw-grass	Saw-grass	<i>Cladium jamaicense</i>	S	2.5
Crab Shell	various	various	S	2.2
Juniper Berry	Eastern Red Cedar	<i>Juniperus virginiana</i>	S	2.2
<i>Smilax</i> Rhizome	Greenbriar	<i>Smilax</i> spp.	S	2.2
Detritus	N/A	N/A	I	0.8
Grass	N/A	N/A	S	0.7
Insect	N/A	N/A	I	0.6
Snail Shell	Florida Marsh Snail	<i>Detracia floridana</i>	I*	0.3
	Olive Nerite	<i>Vitta usnea (Neritina reclivata)</i>		
White Slime	?	?	I	0.3
Hair	rodent and canine	N/A	I*	0.2
Mussel Shell	Atlantic Ribbed Mussel	<i>Geukensia demissa</i>	I	0.2
Clam Shell	Carolina Marsh Clam	<i>Polymesoda caroliniana</i>	I	T
Bulrush Shoot	American Bulrush	<i>Schoenoplectus (Scirpus) americanus</i>	I	T
Sugarberry (seed)	Sugarberry	<i>Celtis laevigata</i>	I	T
Herb Leaf	?	?	I	T

S = Selected food (found as >12% in a single sample, the highest level attained by detritus)

I = Incidental food (always < 12%)

I\* = Food defined as 'incidental' but likely selected for in at least one sample

T = Trace, present but not detected in the point sampling

The stable isotope data were consistent with the fecal data. The isotopic signature of the coastal hog diet matched that of bulrush rhizomes with no deviation caused by a significant dietary fraction missed in the fecal analysis (Figure 4-3). The carbon signals in the apatite and collagen fractions were highly correlated ( $r_s = 0.86$ ,  $p \ll 0.001$ ; Figure 4-4) with no indication of a source of protein different from the major source of energy, consistent with a diet dominated by a single food. There was a significant negative correlation between age rank and  $\delta^{15}\text{N}$  ( $r_s = -0.7$ , one-tailed  $p = 0.018$ ,  $n = 9$ ; Figure 4-5), indicating that some of the spread in  $\delta^{15}\text{N}$  values is due to an enrichment from nursing and the subsequent life-long remodeling of bone.

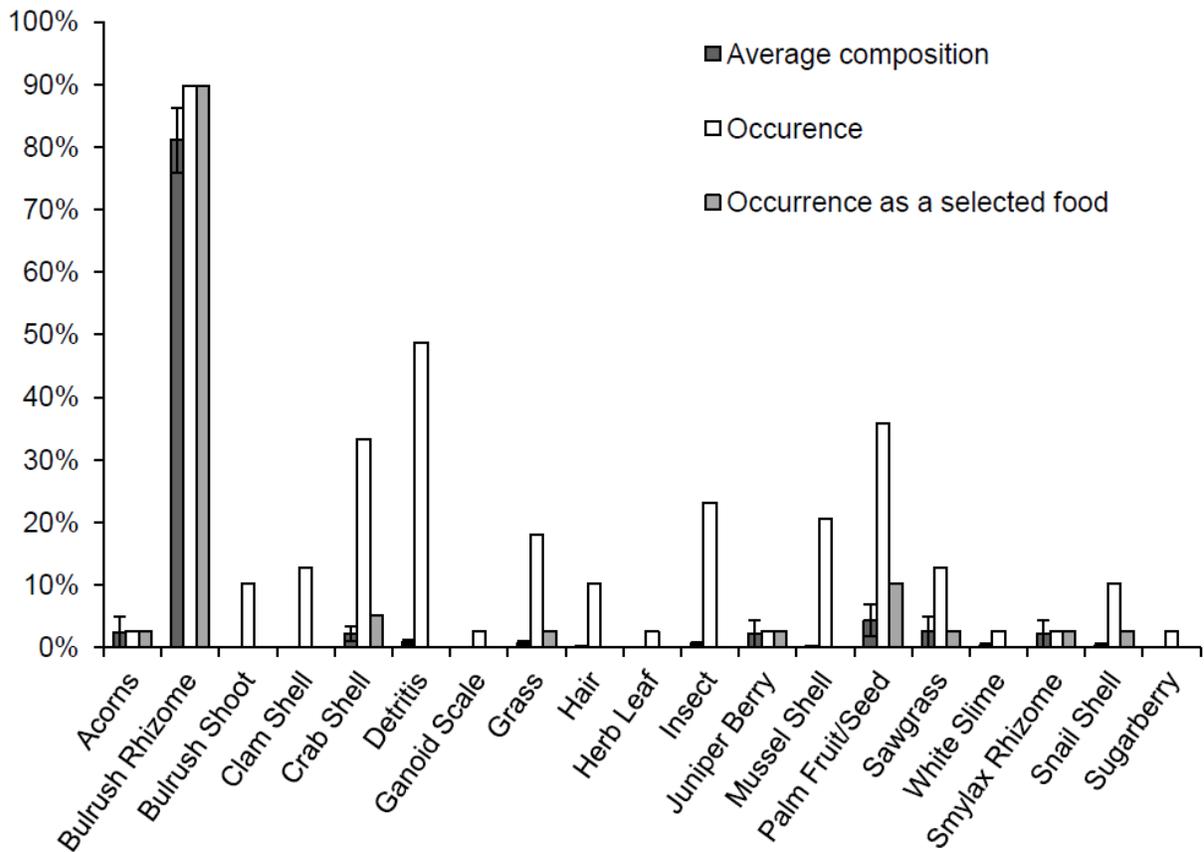


Figure 4-2. Diet of coastal Feral Hogs in the Lower Suwannee National Wildlife Refuge, Florida based on analysis of fecal contents. As 12% was the highest amount of detritus found in any sample, foods found at greater amounts were considered to have been selected for during feeding. Standard errors are indicated.

The stable isotope signatures of coastal hogs (n = 12) are similar to the signatures of hogs from inland Florida (n = 10) for  $\delta^{15}\text{N}$  (t = 0.3, two-tailed p = 0.79) but distinct for  $\delta^{13}\text{C}$  (apatite: t = 4.3, two-tailed p = 0.002; collagen: Wilcoxon sum rank S = 173, p < 0.001) (Figure 4-6). The inland hogs that were the closest to the coast had among the most divergent signatures, implying little movement perpendicular to the coast by individuals. The  $\delta^{13}\text{C}$  signatures imply that the diet of the coastal hogs averages 0% C<sub>4</sub> plants (SD = 7%, range: -10 to 14%) and the diet of the inland hogs averages 57% C<sub>4</sub> plants (SD = 38%, range: 7 to 101%) or 46% maize (SD = 31%, range: 6 to 83%).

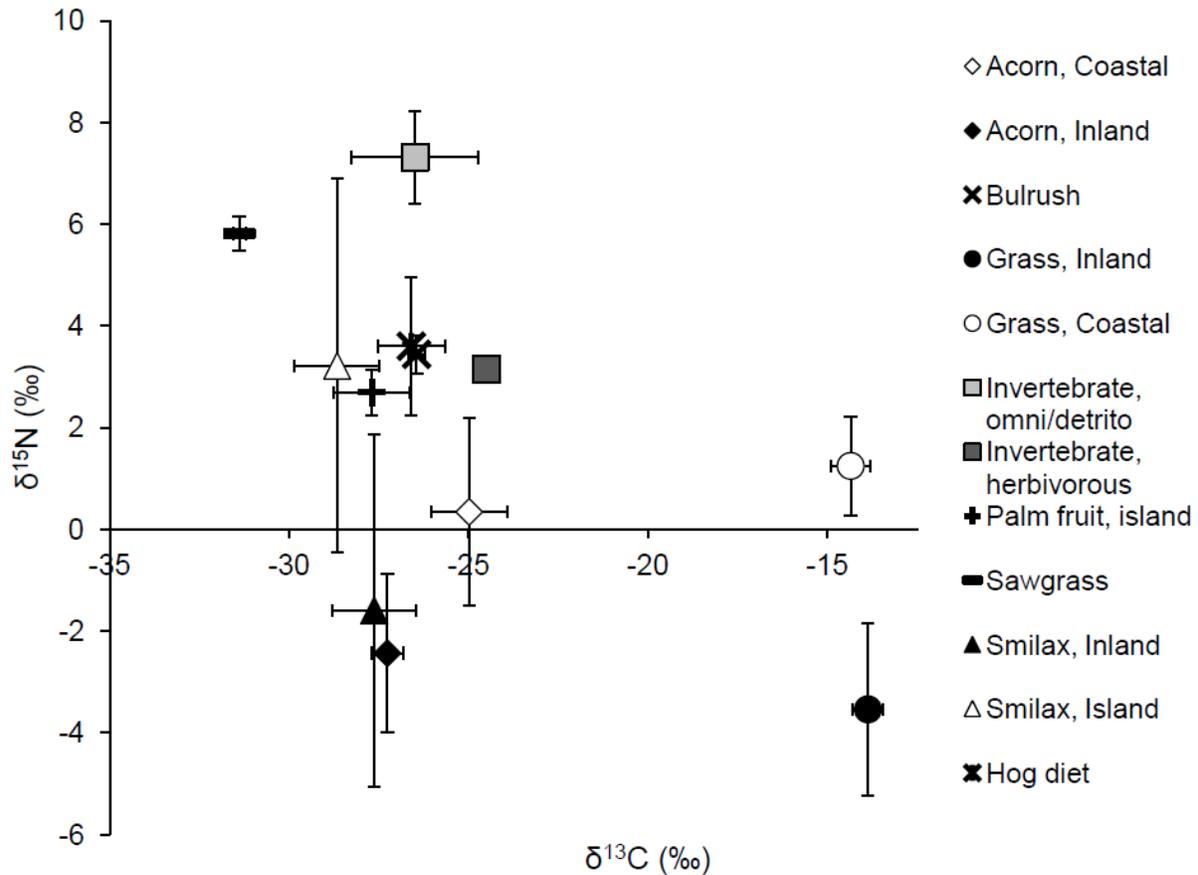


Figure 4-3. Stable isotope signatures of potential food resources and the diet of coastal Feral Hogs in the Lower Suwannee National Wildlife Refuge, Florida. Standard deviations are indicated.

Compared to other vertebrates, Feral Hogs appear to be slightly more enriched in  $^{15}\text{N}$  than herbivores (deer and cattle) and fairly depleted compared to pure carnivores (the otter and alligator) and even other omnivores (rats, raccoons, and opossums) (Figure 4-7). This seems at first glance to indicate an intermediate trophic position; however, it is more likely due to the enriched  $\delta^{15}\text{N}$  values of bulrush (the primary hog food) compared to some of the other plants, including the grasses. As expected, the browser herbivore (deer) seems to have an entirely  $\text{C}_3$  derived diet ( $\text{C}_4$  derived average = -4%, SD = 5%, n = 3) while the grazer herbivore (cattle) has a large dietary fraction made from  $\text{C}_4$  grasses (average = 66%, SD = 25%, n = 3).

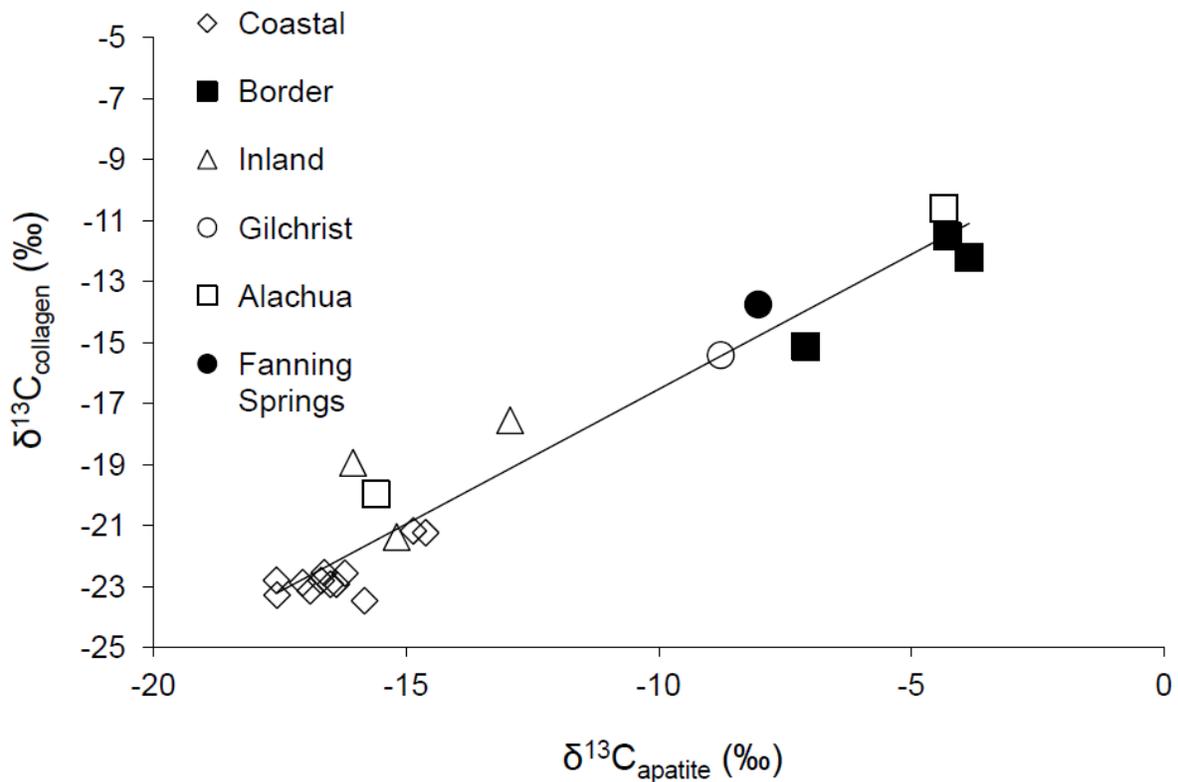


Figure 4-4. A comparison of the stable carbon isotope signatures from bone apatite and bone collagen for the individual hogs used in this study. The two measures are highly correlated indicating that differing sources of protein and energy are not detected.

There was a significant pattern of  $^{15}\text{N}$  depletion in vegetation with increasing distance from the ocean (Figures 4-8 and 4-9) ( $n = 34$ ,  $r_s = -0.79$ ,  $p \ll 0.001$ ) after correcting for the mean  $\delta^{15}\text{N}$  values of the different species.

### Nutrient deposition

Fecal counts were significantly higher on the islands than on the mainland during each sampling period (summer 2005, fall 2005, winter 2005-6, and spring 2006; Wilcoxon sum rank tests, all  $p \ll 0.001$ ) (Figure 4-10). Overall, the island fecal load averaged  $7.9$  fecal piles/ $100 \text{ m}^2 \pm 0.0004$  SE and the mainland fecal load averaged  $1.8$  fecal piles/ $100 \text{ m}^2 \pm 0.0002$  SE; a fecal load 4.4 times higher on the islands than the

mainland. Thus the islands are likely receiving 81% of the nutrients being deposited by the hogs in the hammock and the mainland is receiving 19%.

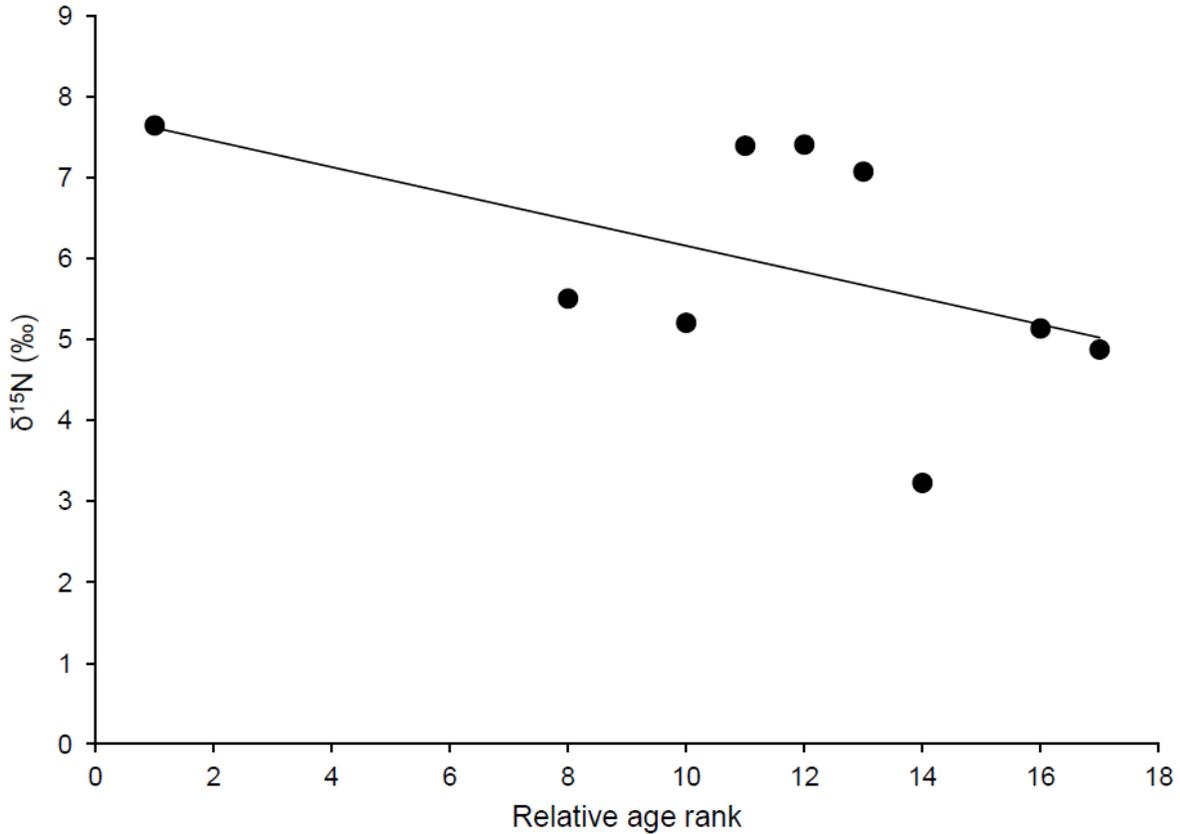


Figure 4-5. The relationship between relative age rank based on tooth eruption and wear of coastal Feral Hogs and  $\delta^{15}\text{N}$  in the Lower Suwannee National Wildlife Refuge. This negative relationship indicates an elevated  $\delta^{15}\text{N}$  signal from suckling that diminishes gradually with age ( $r_s = -0.7$ , one-tailed  $p = 0.018$ ).

The average N, P, and K content of hog feces, and estimated nutrient deposition rates for the islands and coastal mainland are given in Table 4-3.

### Soil and Vegetation Nutrients

The pre-treatment levels of nitrate/nitrite nitrogen, phosphorus, and potassium were significantly higher in the coastal hammock islands in the marsh than on the mainland (Wilcoxon sum rank:  $\text{NO}_x\text{-N}$ :  $S = 1714$ ,  $p = 0.007$ ; P:  $S = 1650$ ,  $p = 0.001$ ; K:  $S$

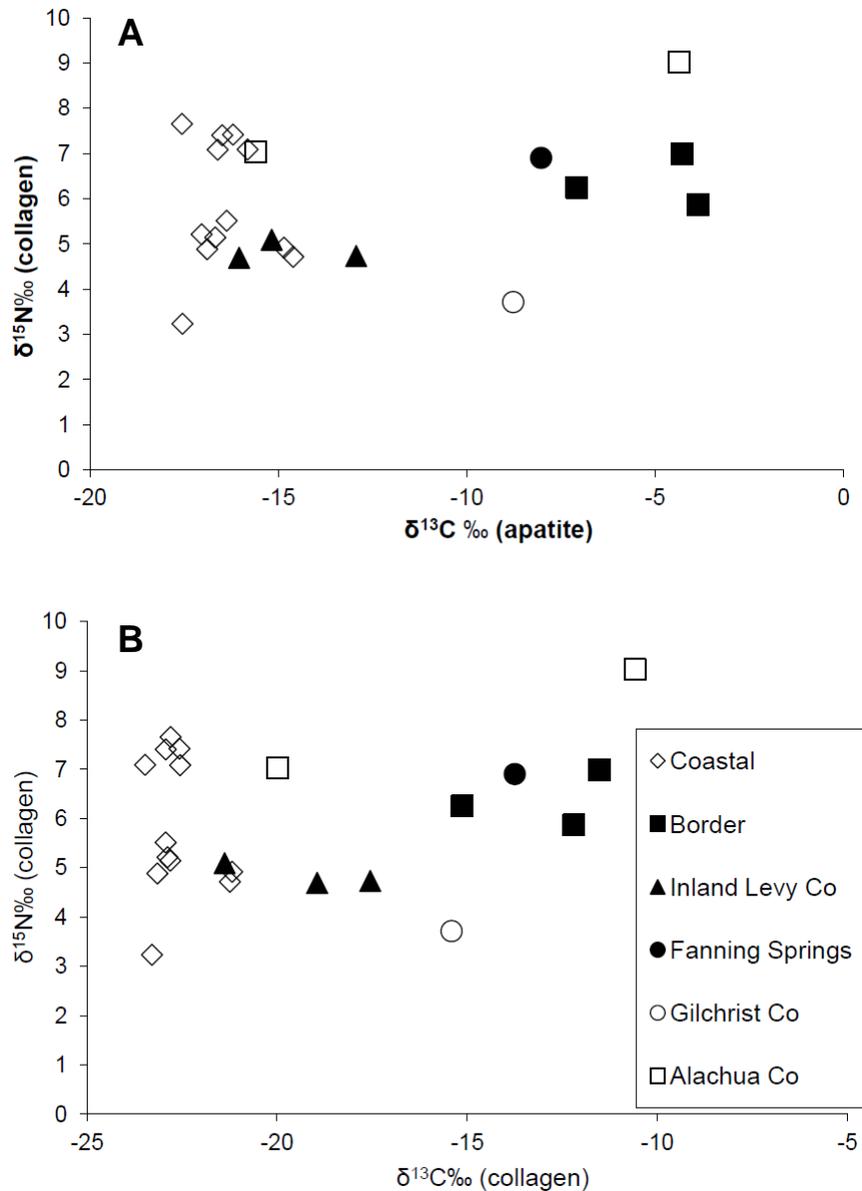


Figure 4-6. Stable isotope signatures of coastal Feral Hog and inland Feral Hog individuals. A) The  $\delta^{15}\text{N}$  signature from collagen and the  $\delta^{13}\text{C}$  signature from apatite. B) The  $\delta^{15}\text{N}$  signature and  $\delta^{13}\text{C}$  signature from collagen. ‘Border’ hogs were from Levy County Road 347 that forms an eastern border of the refuge, ~3-5 km from the coast. ‘Inland Levy County’ hogs were found farther inland on CR 347, ~20 km from the coast. The ‘Fanning Springs’ hog was from ~30 km from the coast and ~35 km from the study site. The ‘Gilchrist Co’ hog was from ~50 km from the coast and study site. The ‘Alachua Co’ hogs were from ~90 km from the coast, although the provenance of the more  $^{13}\text{C}$  depleted specimen was not specified beyond the county level. Note that the inland hogs geographically closest to the coastal hogs have isotopic signatures that are among the furthest from those of the coastal hogs.

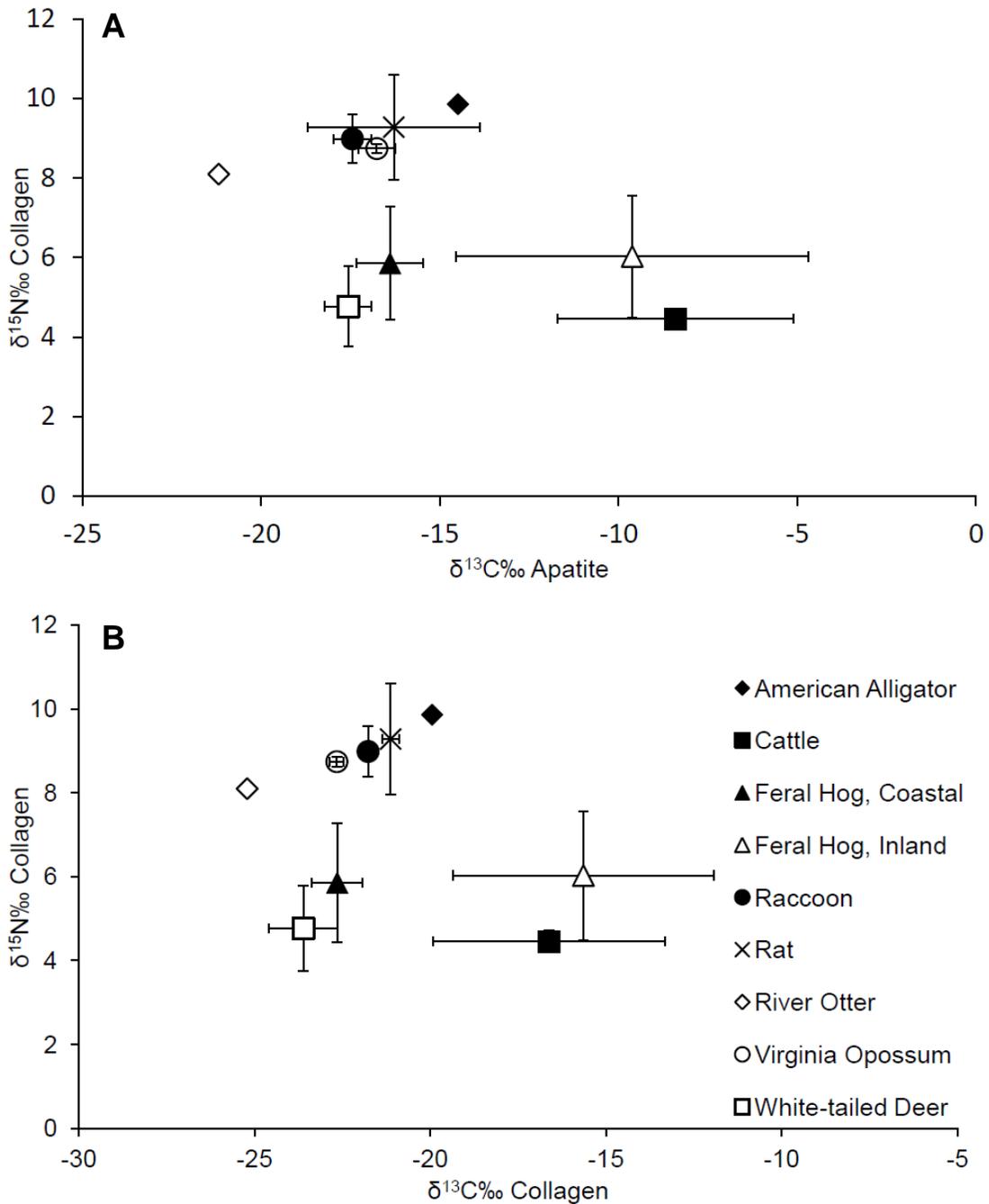


Figure 4-7. Stable isotope signatures of Feral Hogs compared to those of other vertebrates. A) The  $\delta^{15}\text{N}$  signature from collagen and the  $\delta^{13}\text{C}$  signature from apatite. B) The  $\delta^{15}\text{N}$  signature and  $\delta^{13}\text{C}$  signature from collagen. All samples are from the coastal hammock or marsh except for the inland hogs and the otter specimen, which was from CR 347 on the eastern border of the refuge, 9 km from the study site and 0.5 km from the Suwannee River. The hog data are collapsed from Figure 4-6. Standard deviations are indicated.

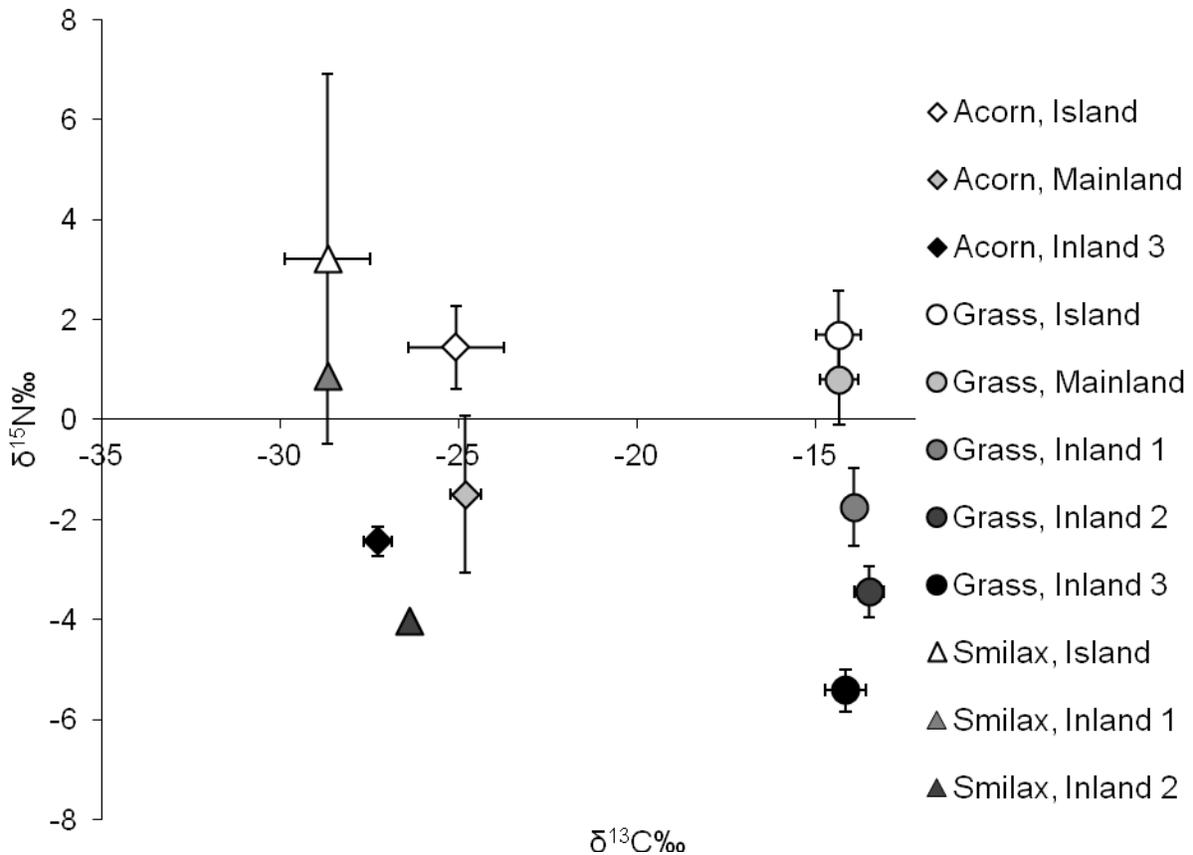


Figure 4-8. Depletion of  $^{15}\text{N}$  with distance from the ocean across different species of plants. The distance from the ocean is  $\sim 4.2$  km for the islands,  $\sim 4.8$  km for the mainland,  $\sim 5.1$  for inland point 1,  $\sim 5.8$  for inland point 2, and  $\sim 6.7$  for inland point 3. Standard deviations are indicated.

= 1418,  $p < 0.001$ ;  $n = 90$ ) (Figure 4-11). Unexpectedly, there were no clear treatment effects of hog exclosure or tilling on the soil richness of any of the three nutrients examined (Figure 4-12).

Contrary to the soil nutrient results, the nutrient content of the biomass was affected by hog exclosure. The phosphorus content of the herbaceous community biomass in the plots overall averaged 1.1 mg/g and ranged from 0.4 – 3.2 mg/g. The island controls had higher P levels than the mainland controls (island:  $1.4 \pm 0.18$  SE; mainland:  $1.0 \pm 0.08$ ; Wilcoxon sum rank  $S = 239$ , one-tailed  $p = 0.01$ ). Tilling had no

long-term observable effect compared to the controls. Exclusion of hogs lowered P in the herbaceous biomass by 0.3 mg/g on the islands but had no effect on the mainland (Figure 4-13).

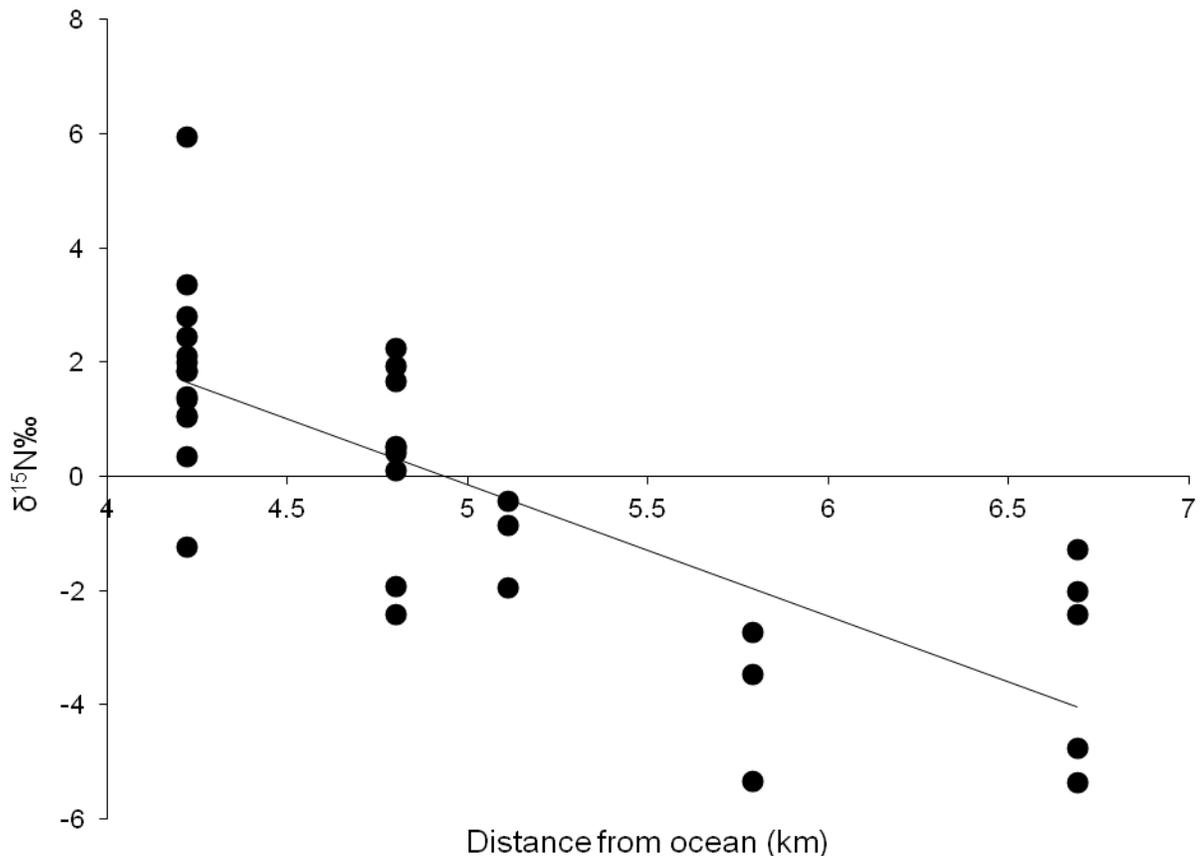


Figure 4-9. The relationship between  $\delta^{15}\text{N}$  of the vegetation and distance from the ocean in the Lower Suwannee National Wildlife Refuge, Florida.

The potassium content of the herbaceous community biomass in the plots overall averaged 12.9 mg/g and ranged from 4.1 – 25.6 mg/g. The island and mainland control K levels were not significantly different (island:  $14.4 \pm 1.8$  SE; mainland:  $12.0 \pm 0.9$ ;  $t = 1.2$ , one-tailed  $p = 0.12$ ). Tilling had no long-term observable effect compared to the controls. Exclusion of hogs lowered K in the herbaceous biomass by 3.0 mg/g on the islands but had no effect on the mainland (Figure 4-13).

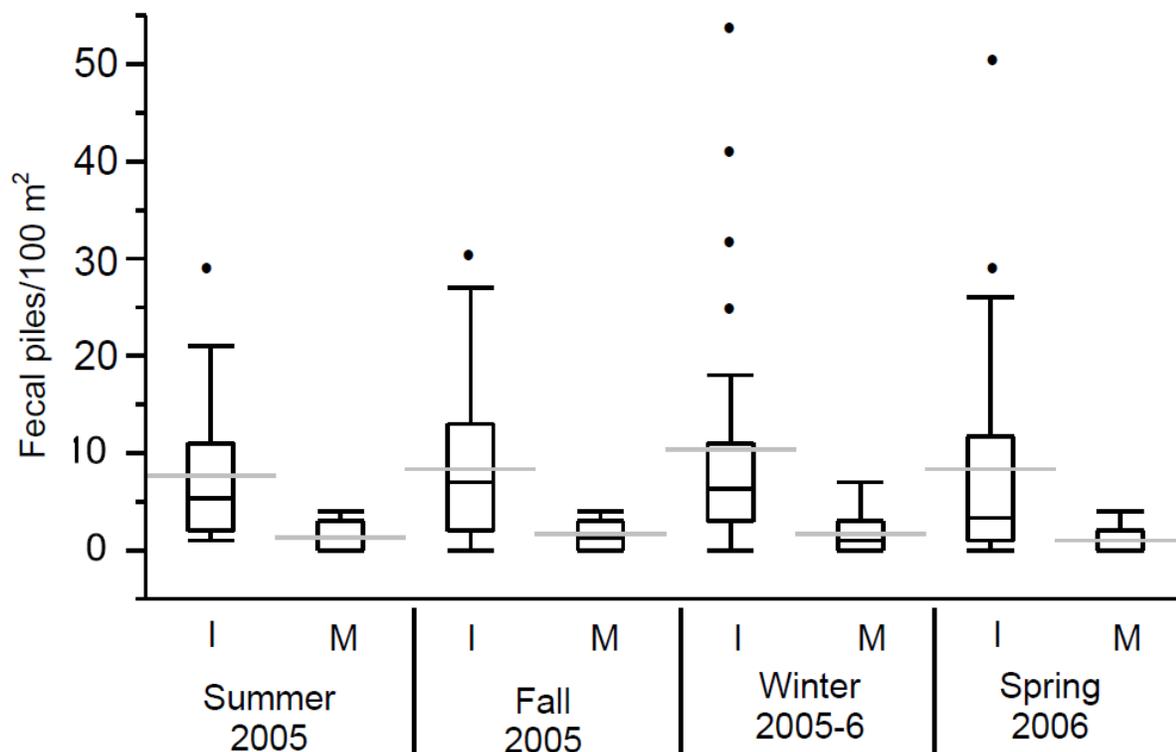


Figure 4-10. Feral Hog fecal load in a coastal hammock community on the mainland (M) as well as isolated hammock islands (I) in the tidal marsh in the Lower Suwannee National Wildlife Refuge, Florida. The lines in the boxes indicate the medians, the boxes indicate the 25<sup>th</sup> and 75<sup>th</sup> percentiles, and the whiskers indicate the last sample within 1.5 times the interquartile distance. Samples outside that range are indicated with dots. Means are indicated by the horizontal gray lines. The fecal loads in each season are significantly higher on the islands.

The total Kjeldahl nitrogen (TKN) of the herbaceous community biomass in the plots overall averaged 12.7 mg/g and ranged from 5.0 – 26.2 mg/g. The island controls had a trend towards higher TKN than the mainland controls (island: 14.9 ±1.3 SE; mainland: 12.4 ±0.9 SE;  $t = 1.55$ , one-tailed  $p = 0.07$ ). Tilling had no long-term observable effect compared to the controls. Exclusion of hogs lowered TKN in the herbaceous biomass by 3.3 mg/g on the islands but had no effect on the mainland (Figure 4-13).

Table 4-3. Estimated (N, P, K) deposition rates on the island and mainland coastal areas by Feral Hogs in the Lower Suwannee National Wildlife Refuge.

Nutrient	% of feces <sup>1</sup>	Fecal deposition (kg/km <sup>2</sup> /year)		Urine:Feces ratio <sup>2</sup>	Urine deposition (kg/ km <sup>2</sup> /year)		Total deposition (kg/ km <sup>2</sup> /year)	
		Island	Mainland		Island	Mainland	Island	Mainland
N	0.42 ±0.04 <sup>3</sup>	2.71 ±0.71	0.64 ±0.17	2.75 ±0.45	7.45 ±4.94	1.75 ±1.25	10.16 ±4.99	2.38 ±1.26
P	0.17 ±0.02	1.10 ±0.24	0.26 ±0.06	0.54 ±0.09	0.59 ±0.28	0.14 ±0.07	1.69 ±0.37	0.40 ±0.09
K	0.14 ±0.01	0.90 ±0.19	0.21 ±0.05	3.25 ±0.16	2.94 ±0.69	0.69 ±0.22	3.84 ±0.72	0.90 ±0.22

<sup>1</sup>By wet weight

<sup>2</sup>The ratios of the amounts of the nutrients excreted through urine and feces based on hog nutrient budgets (Kephart & Sherritt 1990; Sands et al. 2001)

<sup>3</sup>Standard error

Taken as a whole, the nutrient content in the herbaceous biomass showed the same patterns for all three nutrients: the mainland biomass was generally lower than island biomass. Additionally, hog exclosures on the islands resulted in nutrient levels lowered to the levels found on the mainland making two fairly distinct groups: 1) the island controls and island tilled plots and 2) the island exclosures, mainland controls, mainland tilled plots, and mainland exclosures (Figure 4-14).

### Population structure

A total of 162 sightings of hogs allowed classification according to coat color: 102 on the coast, 25 in the non-coastal portion of the refuge, and 35 inland from the refuge. The frequencies of hog colors were different among the three locations (Yate's  $X^2 = 37.2$ ,  $p << 0.001$ ), with the coastal and refuge hogs different from the inland hogs but not from each other (C/I: Yate's  $X^2 = 36.1$ ,  $p << 0.001$ ; I/R: Yate's  $X^2 = 10.9$ ,  $p = 0.012$ ; C/R: Yate's  $X^2 = 0.87$ ,  $p = 0.83$ ) (Figure 4-15). Black was by far the most common color on the coast and in the refuge but the color distribution was more equitable inland,

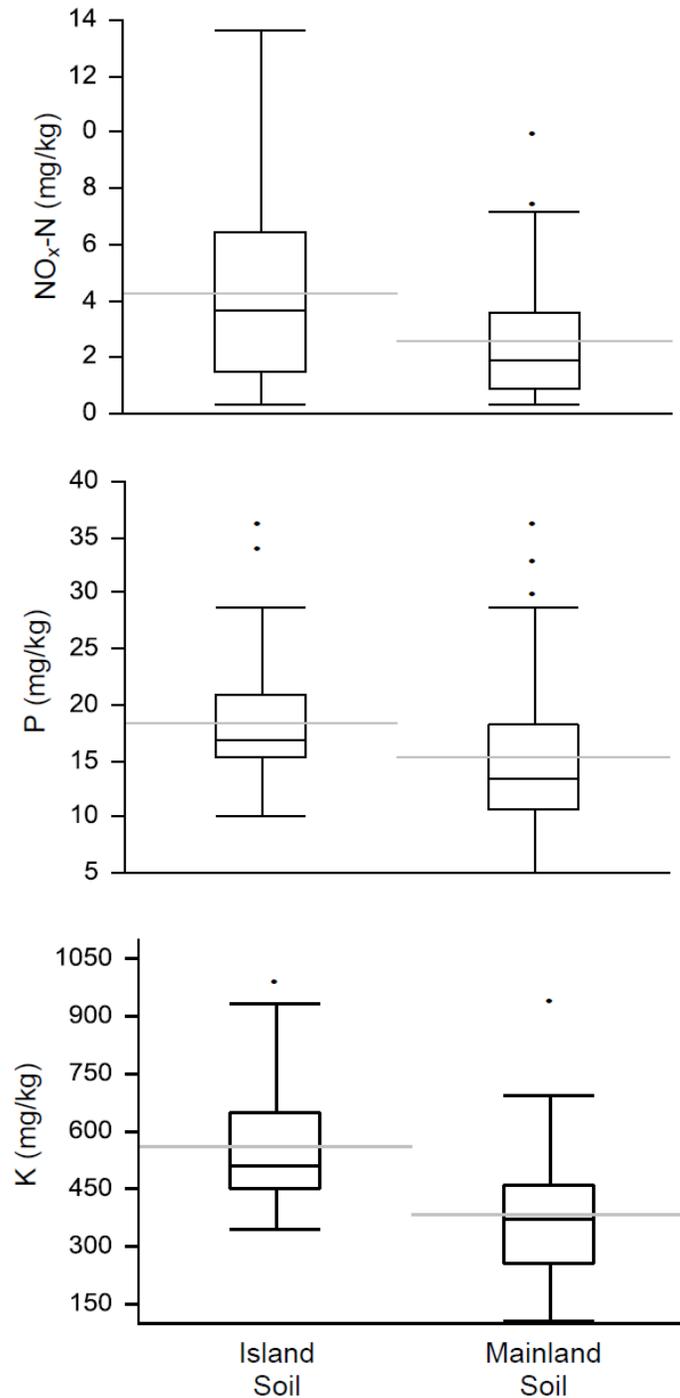


Figure 4-11. Pre-treatment nutrient richness of coastal hammock soils in the Lower Suwannee National Wildlife Refuge from summer 2007. Levels of all three nutrients, nitrate/nitrite nitrogen, phosphorus, and potassium, are significantly higher on the islands in the tidal marsh than on the mainland. Box plots are as in Figure 4-10.

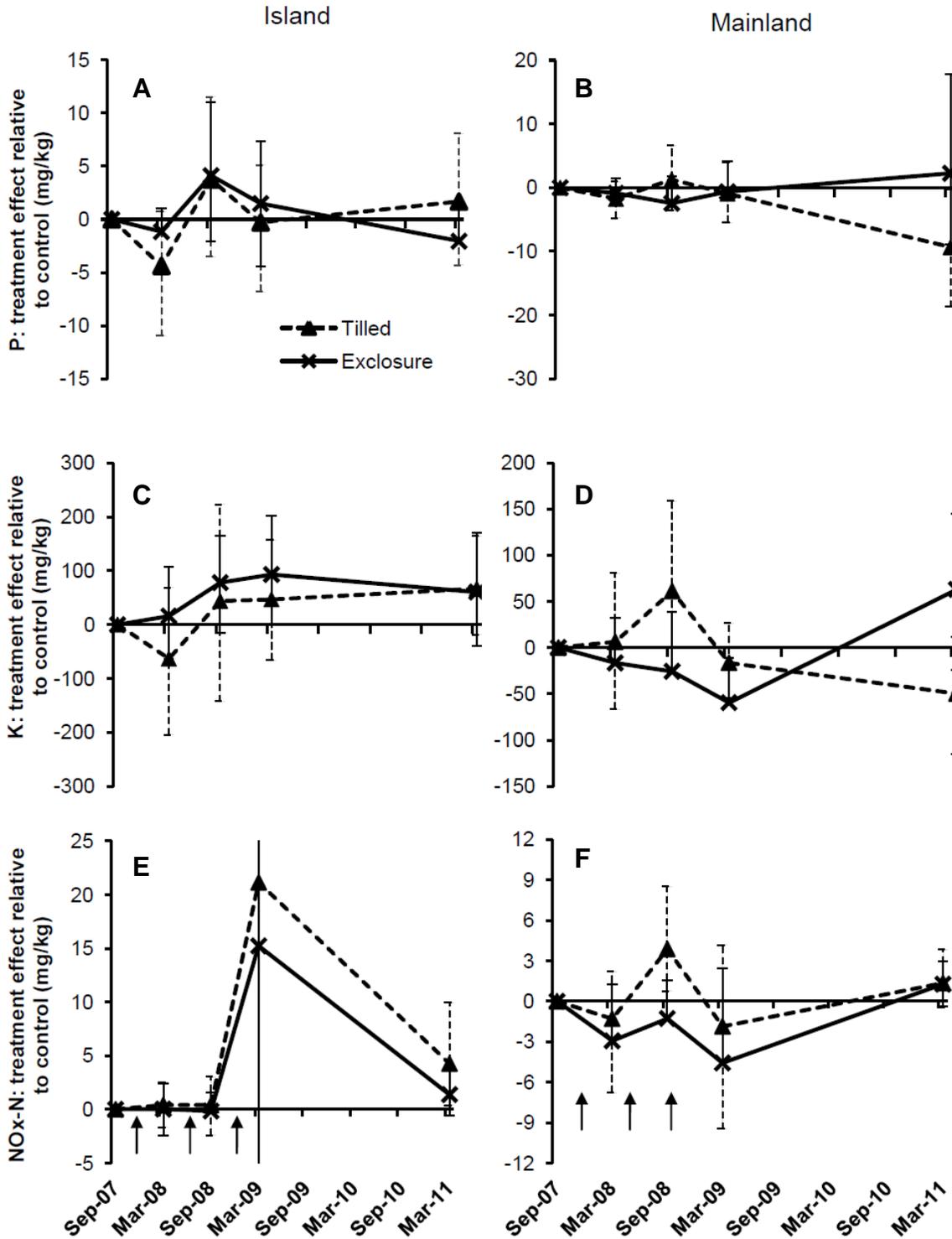


Figure 4-12. Changes in phosphorus, potassium, and nitrate/nitrite nitrogen in the soil in the tilled and exclosure plots compared to the paired controls in island and mainland coastal hammock forests in the Lower Suwannee National Wildlife Refuge, Florida. Arrows (E and F) indicate tilling events to mimic increase hog rooting. 95% confidence intervals are indicated.

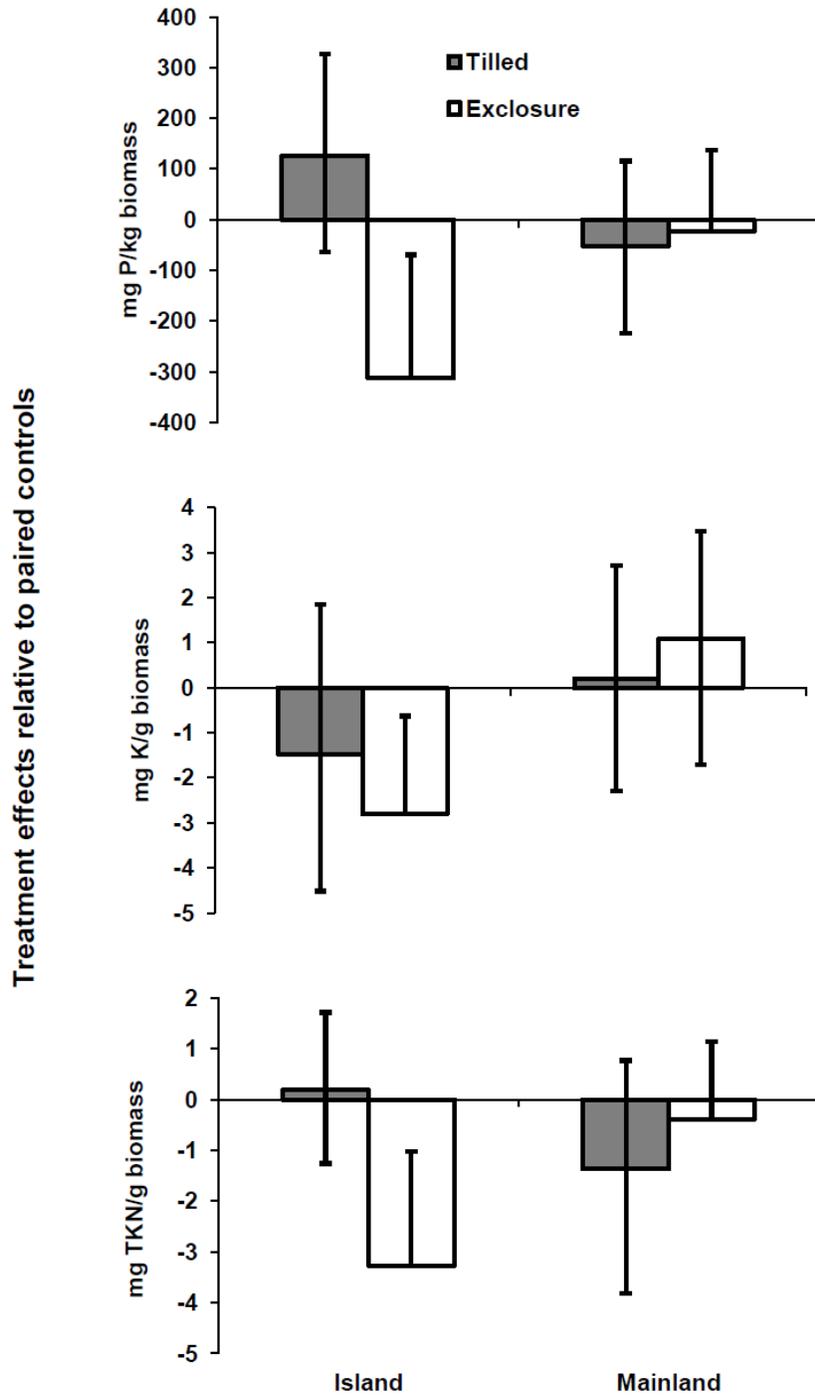


Figure 4-13. The treatment effect relative to paired control plots of 3.5 years of hog exclosures and periodic soil disturbance on phosphorus, potassium, and total Kjeldahl nitrogen (TKN) in herbaceous community biomass. 95% bootstrapping confidence intervals are indicated. Note that the effect is the same for each of the nutrients: hog exclusion on the islands reduces the nutrient content of the herbaceous biomass.

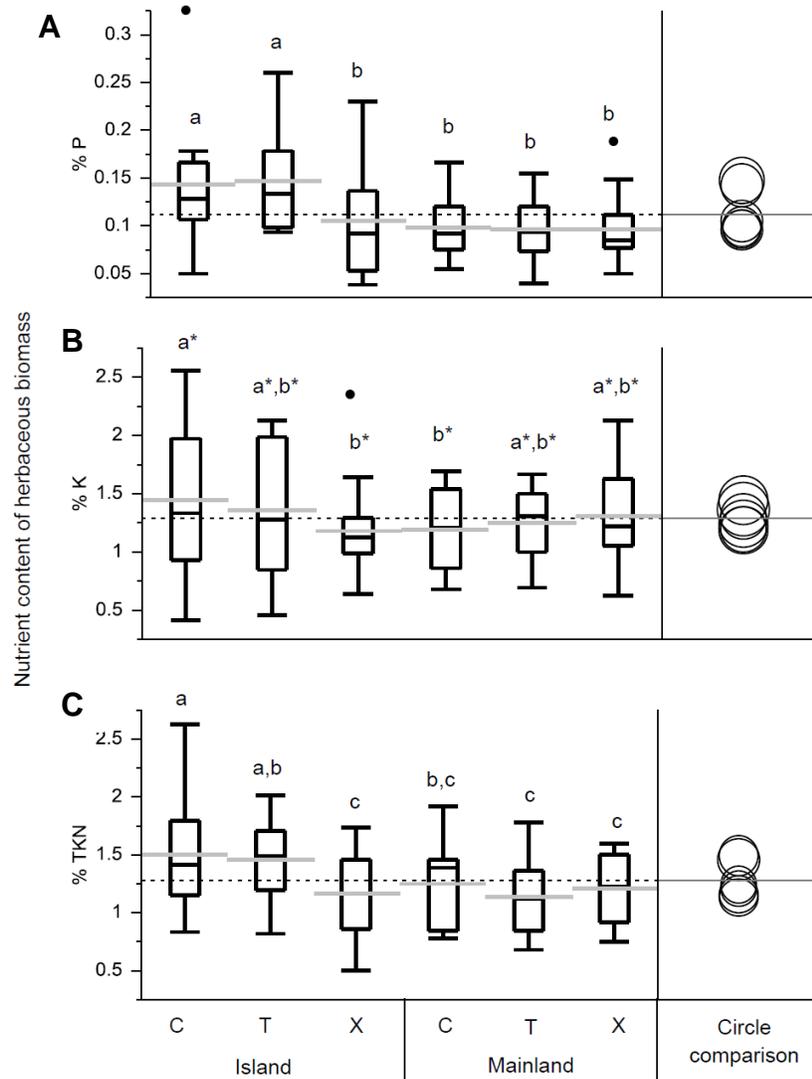


Figure 4-14. Nutrient concentrations in herbaceous community biomass in control, hog enclosure, and soil disturbance (tilled) plots in the coastal hammock on the mainland and isolated islands in the tidal marsh after 3.5 years of treatment and 21 months after the last tilling. The same basic pattern is apparent in all three nutrients (A) phosphorus, B) potassium, and C) total Kjeldahl nitrogen (TKN)): island controls have higher concentrations than mainland controls and hog exclusion on the islands reduces nutrient concentrations to mainland levels but has no effect on the mainland. Tilling appears to have no long-term impact in either area. The main groupings are easily distinguished in the circle comparisons of the same data on the right sides of each panel. The boxes indicate the median and the 25% and 75% quartiles, and the whiskers indicate the last sample within 1.5 times the interquartile distance. Samples outside that range are indicated with dots. Means are indicated by the horizontal gray lines with the total mean indicated by the dotted line. Significant groups are indicated with letters above the boxes.

indicating that the refuge/coastal hogs may be genetically distinct from hogs farther inland. When individual observations were plotted by location, the few samples north of the Suwannee appear to have a lower frequency of black phenotype than the rest of the coast (Figure 4-16).

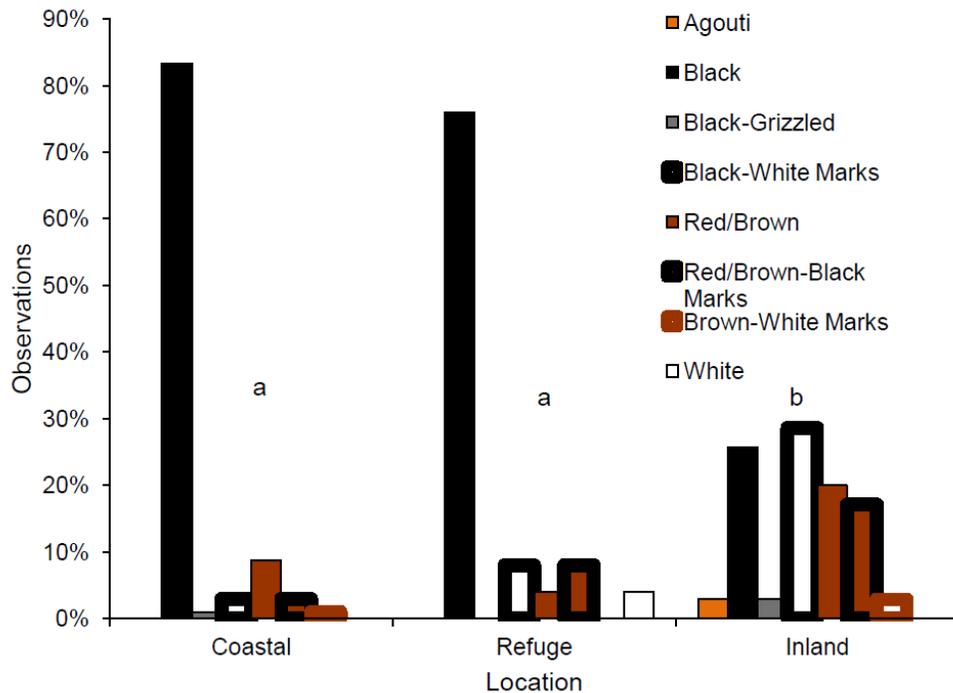


Figure 4-15. Coat color categories of Feral Hogs in and near the Lower Suwannee National Wildlife Refuge. Significant groups are indicated by letters.

Out of 101 fecal samples gathered, microsatellites were amplified from 49 individuals. 27 of the 49 had 9 or more loci characterized. All loci were polymorphic with an average of 8 alleles/locus ( $\pm 2.45$  SD) and a range of 4-12. Heterozygosity ( $H_E$ ) of the loci averaged 7.46 ( $\pm 0.09$  SD) and ranged from 6.24 - 9.22 (Table 4-1). Three genetic groupings were inferred based on  $\Delta K$ . Two were represented only by samples from the study location ( $n = 12$  for Barnett Creek 1 (BC1);  $n = 3$  for Barnett Creek 2 (BC2)) while the last group was represented by individuals within the study location and all the peripheral individuals ( $n = 12$  for General (G)) (Figures 4-17 and 4-18). The

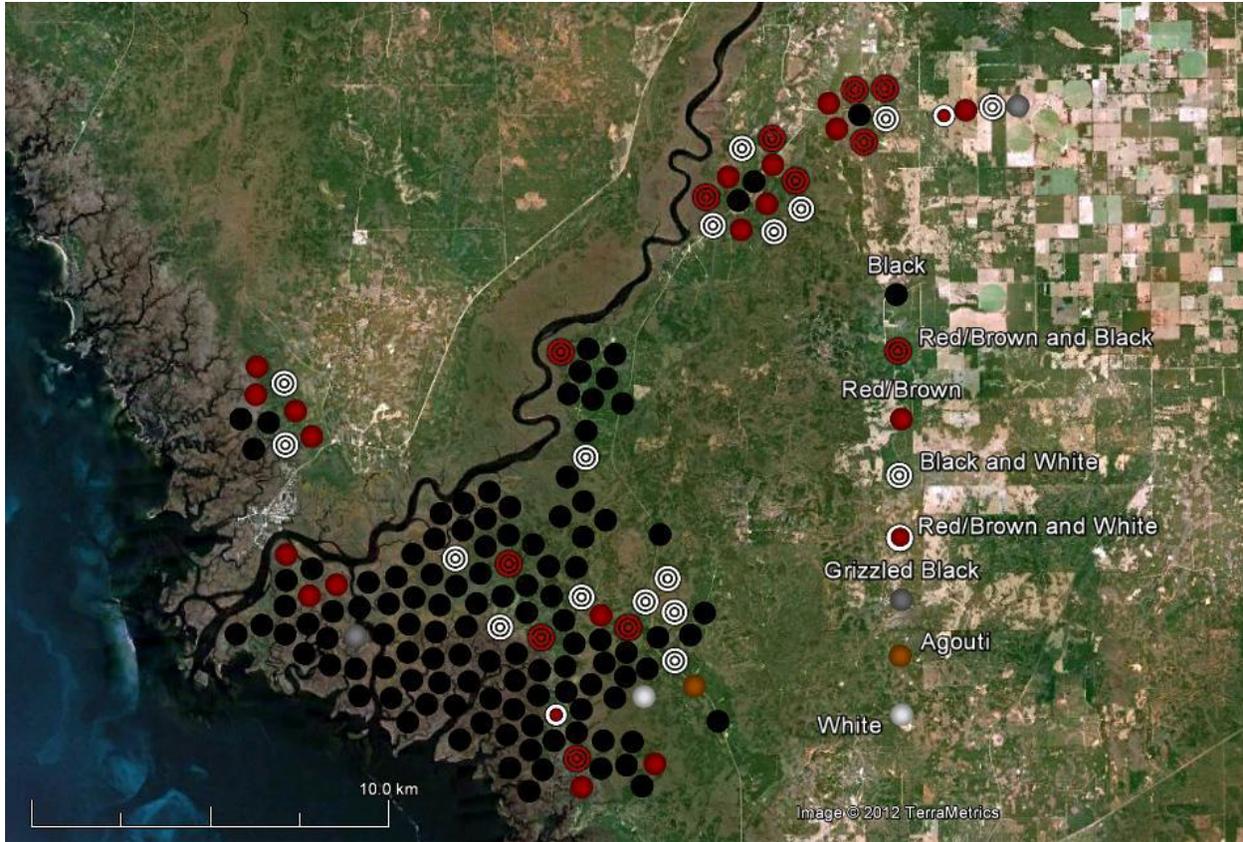


Figure 4-16. Locations of observations of Feral Hogs by coat color. Individual sightings that overlapped due to the scale of the map were spread out for clarity. Most of the coastal observations are clustered around the study site (Figure 4-1) and islands 2 km south of the study site.

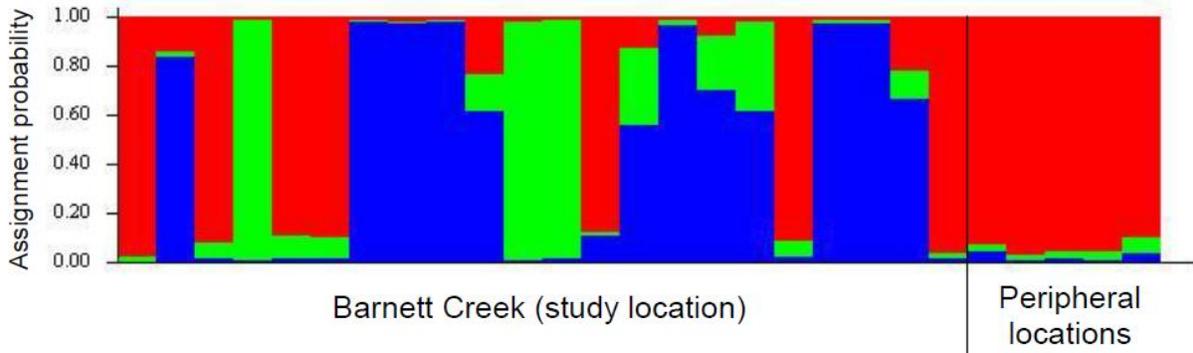


Figure 4-17. Genetic groupings of Feral Hogs in the Lower Suwannee National Wildlife Refuge as determined by STRUCTURE. Barnett Creek runs through the study location. Peripheral samples were taken 2.8 km south-southeast of the study location in the coastal hammock, 6.5 km southeast on the border of the refuge, 6 km north-northeast on the border, 14 km north-northeast, and 8.5 km northwest in the coastal hammock on the other side of the Suwannee River.

fixation index ( $F_{ST}$ ), a measure of genetic differentiation between groups (Wright 1965), was higher between BC1 and BC2 (0.3261) than between BC1 and G (0.1285) and between BC2 and G (0.1326). The genetic differentiation between populations was significant (AMOVA; all  $\Phi_{PT}$ 's  $\geq 0.16$ ; all p's  $\leq 0.008$ ). The mean pair-wise genetic distance between individuals was significantly greater within G than expected and significantly less than expected within BC1 and within BC2 (Figure 4-19). The numbers of migrants/generation between populations were estimated to be 1.3 (G – BC1), 1.2 (G – BC2), and 0.3 (BC1 – BC2). The overall effective population size (for all three genetic groups together) was calculated to be  $792 \pm 131$  SE, which likely reflects an actual adult population size of  $7197 \pm 2422$  SE. Given the estimate of 27 pigs/km<sup>2</sup> used for nutrient deposition rates, this population may cover 200-300 km<sup>2</sup>, essentially the size (though not necessarily the shape) of LSNWR (214 km<sup>2</sup>).

## **Discussion**

### **Diet**

Both the fecal analysis and the stable isotope signatures revealed that American Bulrush dominates the diet of Feral Hogs in the coastal hammock. In spite of this extreme and unexpected specialization on a single food source, the hogs were clearly selectively feeding on other foods from time to time. One sample contained over a dozen Olive Nerite opercula and others contained a great deal of hair so these were not likely to have been incidentally ingested. Also, it was observed during the study that skeletal remains were often surrounded by hog-trampled ground with the smaller skeletal components broken or missing, implying cannibalism.

These observations as well as the fact that minor components in the overall diet often appeared as the major component in a few samples, indicates that the hogs will

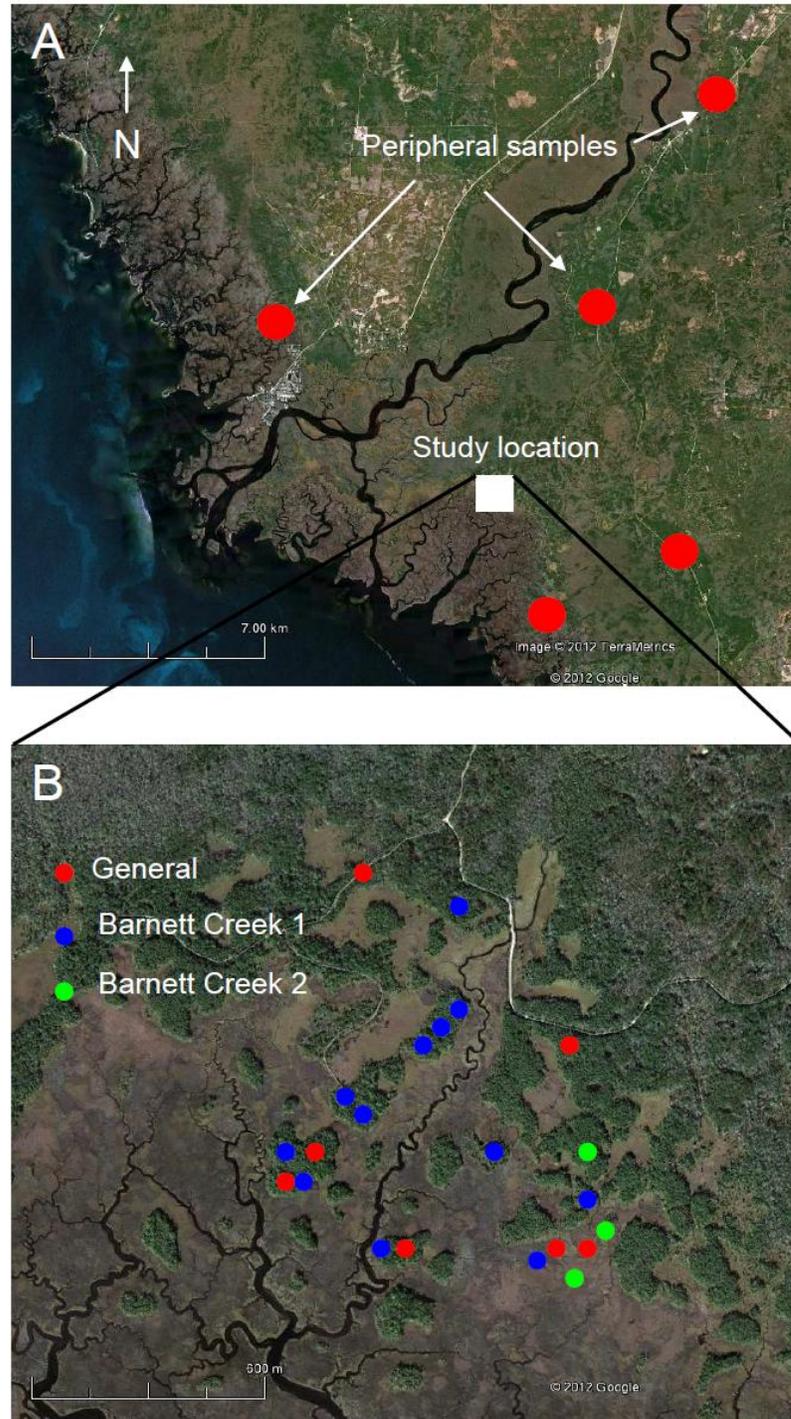


Figure 4-18. Locations and genetic groupings of Feral Hog samples from the Lower Suwannee National Wildlife Refuge and environs. a) Locations of the study and individual peripheral samples. b) Locations of individual samples from the study location. Note that the genetic divisions are not related to geographic divisions. The color coding is the same as in Figure 4-17.

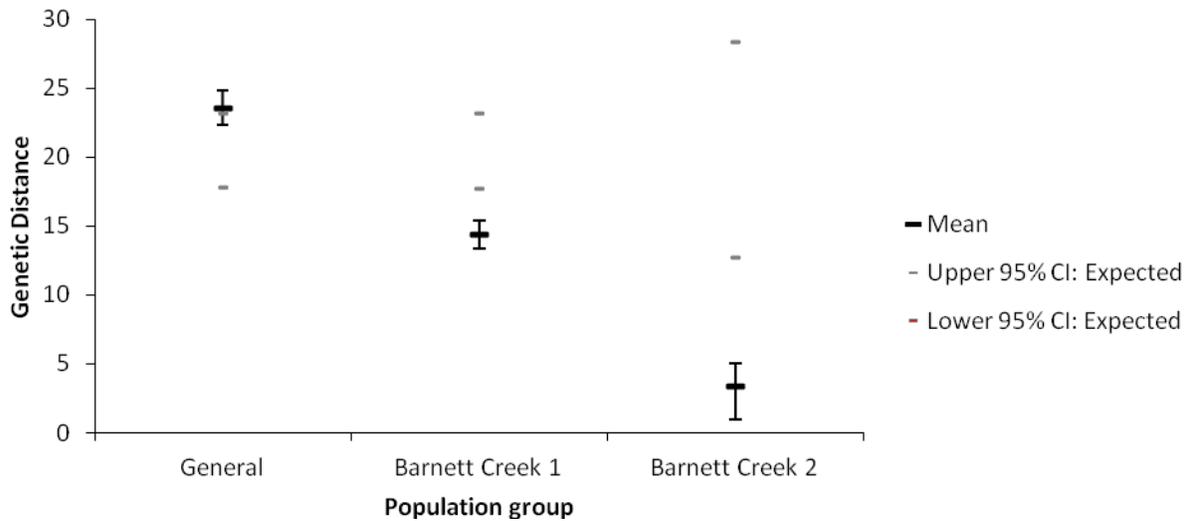


Figure 4-19. Mean pair-wise genetic distances between individuals of the 3 inferred population groupings for Feral Hogs in or near the Lower Suwannee National Wildlife Refuge. 95% confidence intervals determined by bootstrapping are indicated. Error bars are the 95% confidence intervals for the means.

opportunistically forage on other resources periodically (e.g., meat), which may not be detected in fecal analysis. However, the stable isotope data do not indicate that a major dietary component is being missed by the fecal analysis. Because the isotope signature of the hog diet almost perfectly overlays the bulrush signature, any other major fractions would have to be improbably balanced to remain undetected. Therefore, the vast majority of nutrients flowing through the coastal hogs are being sourced from the marsh generally and from American Bulrush specifically.

The enriched  $\delta^{15}\text{N}$  signature in the collagen of younger animals is an expected result of lactating females catabolizing their own tissues to produce milk consumed by their offspring (Newsome et al. 2006; Polischuk et al. 2001; Sare et al. 2005). Females able to lactate using increased food intake rather than body reserves, should not confer an enriched  $\delta^{15}\text{N}$  signature to their young (Jenkins et al. 2001). The observation that lactating females seen during the study were boney and in poor condition (indicating

that lactation required the use of body reserves) is consistent with the negative correlation between  $\delta^{15}\text{N}$  and estimated biological age.

The decreasing gradient in  $\delta^{15}\text{N}$  in plant tissues with increasing distance from the coast is likely due to the sometimes very negative  $\delta^{15}\text{N}$  values in precipitation deposited N ( $\text{NH}_4^+$ : -17 to +4‰,  $\text{NO}_3^-$ : -8 to +8‰; Shearer & Kohl 1992) that is countered based on distance from the coast by the enriched values found in coastal plants caused by marine-deposited nitrogen (+5 to +10‰ higher; Heaton 1987; Virginia & Delwiche 1982) or found in plants grown in saline environments (+4.1‰ higher than non-saline soil; Heaton 1987).

The importance of the marsh as a source of resources likely results in a neighborhood effect that leads to their heavy use of the islands and relative avoidance of the mainland (Figure 4-10 and Chapter 3). The close juxtaposition of food and shelter results in fairly short transport distances, likely on the order of 100 – 200 m (Chapter 3). A third required resource for pigs, wallows (Fernández-Llario 2005), seems to be concentrated in open mud along trails through the marsh or on the shaded border with the hammock where the marsh vegetation cannot grow (pers. obs.) and are thus conveniently accessed from both habitats.

The incorporation of  $\text{C}_4$  plant-derived foods in the diets of non-coastal hogs does not seem to be a result of participation in a  $\text{C}_4$  grass food chain that is absent from the coast. All the grasses measured were  $\text{C}_4$  grasses including two of the most common species in the coastal hammock. Rather, it is likely that the  $\text{C}_4$  resource being consumed is feed corn. The land bordering the refuge and farther inland is largely privately owned hunting and agricultural land including cattle range (pers. obs.). Hogs

outside the refuge are possibly feeding on corn pilfered from cattle operations and, probably more importantly, wildlife feeding stations meant to attract game. Based on observations of discarded feed corn bags, the feeding of wildlife peaks just before hunting season but may also occur year-round to ensure that game animals are permanent residents.

The fact that coastal pigs have very distinct stable isotope signatures from pigs on the border of LSNWF indicates that movement between the coastal hammock and inland areas is not typical and nutrient transport distances from the marsh are short and only go as far as the coastal hammock. This observation suggests that there might be little migration of individuals between the coastal hammock and other areas, which may lead to genetic population structure (discussed below).

### **Nutrient deposition**

The amount of nutrients being transported by the hogs appears to be a fraction of the atmospheric deposition recorded for this region of Florida: N islands: 3%, N mainland: 1% (Hendry et al. 1981); P islands: 7%, P mainland: 2% (Hendry et al. 1981); and K islands: 11%, mainland: 3% (Grimshaw & Dolske 2002). However, because of the centuries-long history of hogs in Florida (Mayer & Brisbin 1991), these small inputs appear to have resulted in an uneven distribution of nutrients in the coastal hammock, with the island soils being richer in nutrients than those on the mainland (Figure 4-11). Additionally, the high rates of denitrification that occur in waterlogged soils (Morris 1991) likely increase the importance of nitrogen deposited by the hogs.

### **Soil and plant nutrients**

The exclosures and tilling treatments did not have clear patterns of effects on the soil nutrients. This may be because the scale of the exclosures was smaller than the

scale at which some soil processes operate or that the treatments were too short in time. The exclosures were built to address questions about the herbaceous community and were far too small to incorporate the root system of mature trees. Tree roots comprised an average of 8% of the dry weight of the soil cores and much greater (unmeasured) weight and volume fractions while fresh. Thus trees with roots both inside and outside an exclosure could have been supplementing tissues inside the exclosures with nutrients brought from richer soils on the outside. When the soil samples were dried and ground, root fragments could have biased the soil results towards the nutrient content of the trees.

Another difficulty with the soil samples is the fact that they were gathered at single points in time. Because the nutrients (especially N) are often mobile in the soils, patterns of rainfall and flooding can add to the unpredictability of nutrient availability caused by animal depositions and other periodic pulses of nutrient flux. This variation likely overwhelmed the once per 6-month soil sampling schedule and confounded the soil richness portion of the experiment.

The exclosures did show that the hogs do have a measurable effect on the nutrient content of the herbaceous biomass, however; even over the four year time-scale of this study. A soil sample is representative of one instant in time so any given sample is not likely to be an accurate measure of the changing nutrient levels available for plant growth, but plant tissue gives much better estimates of the available nutrients as it provides an average of nutrient levels experienced over time (Sartain 2008). Thus while tilling does not have a significant long-term impact on the nitrogen environment

experienced by herbaceous plants, exclusion of hogs does have an impact on the islands but not on the mainland (Figures 4-13 and 4-14).

When hogs are excluded from an island hammock, the nutrient levels in herbaceous biomass drop to levels found on the mainland. This indicates that hogs are important in transporting nutrients to the islands but that the density of hogs on the mainland is small enough that the amounts of N, P, and K deposited there are negligible. It also indicates that the effect is seen fairly quickly in the herbaceous vegetation (within 4 years).

Interestingly, one of the most common herbaceous plants, St. Augustine Grass, is a common turf grass and therefore has fairly well described nutrient requirements. It grows best with access to enough nutrients for 2-3% of its tissues to be nitrogen, 0.15-0.5% phosphorus, and 1-3% potassium (Sartain 2008). To put this in perspective, plant tissues are typically 1.5% N (range: 1-5% in non-woody tissues; Mattson 1980), 0.2% P, and 1.0% K (Billings 1970). It is apparent that in this system some nutrients may be limiting for plant growth (Figure 4-14).

The island non-exclosure biomasses approach typical plant levels of nitrogen content but none reach ideal levels for St. Augustine Grass, while the mainland and island exclosure levels are lower than typical. Because denitrification proceeds apace in waterlogged soils (Morris 1991), in this constantly moist system nitrogen loss is probably severe so additions by hogs are important in maintaining current levels.

Phosphorus levels also seem to be insufficient for ideal growth by St. Augustine Grass. The nutrient content of the plant tissues is below typical for plants in general and below ideal on both the mainland and the island. However, on the islands

phosphorus levels approach the lower end of the range for non-exclosure plots (Figure 4-14A). The soil on the islands is within the lower end of the range required for good growth (Figure 4-11; 16-30 mg/kg; Sartain 2008), but the mainland is even lower.

Potassium levels appear to be adequate for St Augustine Grass and above what is typical for plants in general, as might be expected given that the richness of the soil in potassium (Figure 4-11) exceeds the grass's requirements for ideal growth (36-60 mg/kg; Sartain 2008) by one order of magnitude. The observed increase in K levels in plant tissue on the islands likely has more to do with release from the limitations of other nutrients rather than the higher K levels in the island soils.

### **Population structure**

The stable isotope data suggested that there might be different populations of pigs using the coastal hammock and the rest of LSNWR, at least the inland border of the refuge. The observed hog color frequencies (Figures 4-15 and 4-16), however, suggest that the coastal hammock and refuge hogs might be in a single genetically mixed population (even if individuals rarely move to different habitats during their lifetimes) but the inland hogs might be distinct.

It was expected that coastal hogs should be predominantly black as that color confers protection from the fierce Florida sun while the pigs are foraging in the marsh, but hogs living in fully forested systems, such as the upland pine/hardwood swamp system of the rest of the refuge, should show much more color variation as the selection for sun-protection is relaxed under a canopy (Mayer et al. 1989). This expectation is clearly met when considering the coastal hammock and the inland areas. However the refuge hogs are predominantly black as well. This observation does not necessarily conflict with the expectation for increased selection for black in exposed habitats

because 1) black is likely to be beneficial in a largely forested habitat as it is less visible to predators/hunters and 2) if phenotypes are not or weakly selected in the rest of the refuge, phenotype frequencies there could still be influenced by strong selection on the coast and migration between the two areas.

Interestingly, the black phenotype does not appear to be dominant in frequency in the few observations north of the Suwannee River (Figure 4-16), contrary to expectations. This might be due to an influx of new migrants in the recent past but is more likely to be simply a random effect of a small sample size from that area. The impact of small sample size is exaggerated in this case because the social system of hogs is based on groups of related individuals (sounders) and samples of phenotype from related individuals are not independent of each other. The observations from that location were collected during only two days, so it is possible that all the pigs belonged to only one to three sounders and were highly related.

Of the three genetic groups found in the genetic data, one contained all the peripheral pigs and some pigs from the study location while the other two were found only in the study location but intermingled geographically (Figure 4-18). The two groups from the study location, BC1 and BC2, are probably sounders composed of closely related individuals. In other populations of Feral Hogs, sounders are distinct enough genetically to be detected with similar methods to those used here (Spencer et al. 2005). The General group (G) is very unlikely to be a single thoroughly well-traveled sounder. Rather, G is probably composed of individuals from different sounders. Because STRUCTURE was not able to group any of those hogs with any others from the same sounder, it created a general group that encompassed all hogs from sounders

with only one representative and two groups with hogs from sounders with multiple representatives.

This interpretation is supported by the  $F_{ST}$  values among groups: the sounders are more distinct from each other than they are from a group that includes members of multiple sounders from the general population. Because each sounder probably has its own distinct familial genetic profiles, it is less similar to another sounder than to a group made of genetically diverse members of the general population. The intra-group pairwise genetic distances also support the two sounders within a larger population conclusion. Any two individuals from the general population are more genetically different than expected based on the entire population structure while any two individuals from the sounders are more similar than expected (Figure 4-19).

These results must be treated with caution, however, due to the small number of individuals in BC2 and the lack of resolution in the general population. The scale of genetic differentiation detected was much finer in resolution (between sounders) than required in this study (between populations in geographic areas). In order to fully tease out the inter-sounder population structure hinted at by the stable isotope and color frequency data, a much more intensive and complete sampling regime will be needed with multiple samples from each sounder.

The population estimate, 7197  $\pm$ 2422 SE pigs, seems reasonable considering that this region of Florida has long been known as having an extremely high density of Feral Hogs (Mayer & Brisbin 1991). However, given the assumptions of estimating an effective population size, it is likely that this population estimate should be taken as an upper limit. The method used to estimate effective population size assumes that the

equilibrium has been reached between addition of new alleles through mutation and extinction of alleles through genetic drift (Frankham 1996). This process takes a great deal of time. For example, the effective population of humans is estimated from molecular data to be ~10,000. This excessively low estimate is a signature from past bottlenecks in human populations and not an accurate gauge of modern  $N_e$  (Charlesworth 2009).

In the case of Feral Hogs along the Gulf Coast, they are likely derived from multiple lines of domestic hogs introduced to Florida multiple times since Hernando de Soto first introduced them in 1539 (Towne & Wentworth 1950). Until the 1960s, Florida had an open range law that allowed livestock owners to let their animals roam free throughout the landscape and a continual source of novel alleles for the feral population (Mayer & Brisbin 1991). Even if each breed has low genetic diversity, a population derived from multiple breeds from around the world has the potential to hold much greater genetic variation than would be expected based on population size (Laval et al. 2000).

### **The Ecology of Feral Hogs**

Feral Hogs have strong impacts on the biomass and species richness of the coastal hammock herbaceous community (Chapter 3) and, as evidenced by this chapter, they also influence the nutrient status of the herbaceous community through deposition of marsh-derived nutrients in the coastal hammock. Their influence on biomass and perhaps species richness is likely due to an increase in disturbance, which in itself can increase the susceptibility of plants to herbivory by insects (Spiller & Agrawal 2003). However, because of the waterlogged condition of the coastal hammock, oxygen limitation is likely one of the most important limitations on plant

growth. Slight differences in elevation (amounting to centimeters) appear to lead to differences in flooding frequency and exposure to moisture wicked up from lower soil layers and may lead to extreme differences in herbaceous cover when other conditions seem comparable (pers. obs.). Through rooting, hogs may partially mitigate this limitation by aerating the soil, but the direct effect the disturbance has on biomass likely eliminates this benefit in terms of standing crop of biomass (though it might lead to faster recovery from rooting than from a less disruptive form of biomass loss, such as grazing). This may change competitive interactions, *e.g.*, benefiting plants not specifically adapted to waterlogged soils by giving them areas of temporarily increased O<sub>2</sub> availability.

The herbaceous community in this habitat was likely constrained to a great extent by the moist anoxic soil conditions, yet nutrient deposition still had a significant effect on the plants. In less anoxic terrestrial systems, nutrient limitation might play a larger role in restricting plant growth and determining species composition. Therefore nutrient deposition might be even more important in terrestrial systems than it is in the coastal hammock. Nutrient enrichment can also shift competitive interactions among plants (Gaucherand et al. 2006) and favors ruderal species, which are also benefited by disturbance and reduced competition (reduced biomass and reduced species richness). These sorts of changes are typical of anthropogenic influences and favor many exotic species. Thus it is likely that Feral Hogs in this and other systems diminish the resistance of the native communities to compositional changes and invasion by exotic species, not just by the physical disturbance that tends to be the focus of most studies, but also by depositing nutrients derived from rich feeding grounds (wetlands, agricultural

lands, middens, etc.) in refuge habitats that may already be fragmented and vulnerable to biotic invasion and degradation.

Another important aspect of Feral Hog ecology in this system appears to be occurring in the marsh. American Bulrush was observed to grow only in the areas of the marsh rooted by Feral Hogs. Even when the bulrush had been left unrooted long enough to mature, the soil remained more loosely packed and the vegetation much less crowded than in neighboring Black Needlerush or Sawgrass patches. This observation leads to three possible conclusions: 1) either hogs feed only in the bulrush patches, 2) bulrush grows only in hog-rooted areas, 3) both 1 and 2.

If hogs only fed in the bulrush patches, it would be unlikely for the hogs to root the entirety of every patch and the edges of the patches should be unstable as feeding by the hogs should tend to reduce the competitive ability of bulrush compared to other marsh plants. However, no unrooted patches of bulrush were ever found and the bulrush patches are amazingly stable. A comparison of aerial photographs taken over 50 years shows stable patches of rooted bulrush in the same areas (Figure 4-20). In fact, small enclosed patches of needlerush within the bulrush patches are surprisingly stable as well. Because Saw-grass is a fresh/brackish water species (Wunderlin 1998), its patches are usually found along the creek or next to the hammocks. Black Needlerush is a brackish water species (Pennings et al. 2005) and is found (in this area) from the hammock all the way to the ocean. American Bulrush is a brackish/saline water species (Wunderlin 1998) but is only found in hog rooted areas near the coast and islands.

If bulrush only grew in hog-rooted areas, the patches would similarly be unstable as hogs would be creating new bulrush patches as they rooted through the marsh. However, not only are the patches stable but, based on bulrush being the hog's only important dietary component, it is unclear what would drive hogs to root outside bulrush patches.

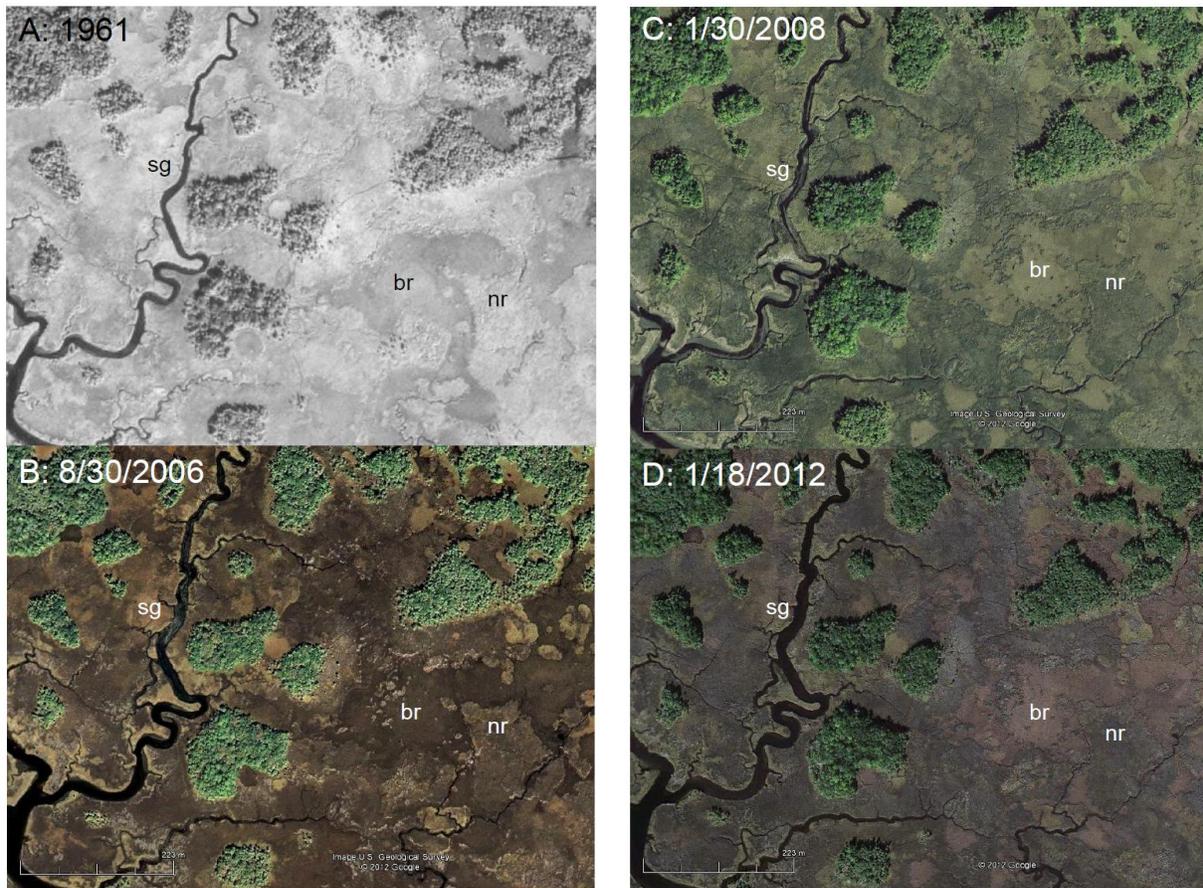


Figure 4-20. Aerial photographs of a portion of the field site showing the spatial stability of the marsh community over time. A) 1961, B) 8/30/2006, C) 1/30/2008, D) 1/18/2012. br = American Bulrush, nr = Black Needlerush, sg = Saw-grass. Patch composition can be identified by coloration and the sharper shadowed border usually found around bulrush patches due to the difference in height and density of the bulrush patches. Color changes with season but needlerush patches are normally a dark green, Saw-grass is usually a light green or yellow-green, and bulrush is normally a light green or brown-green although patches are often very dark if freshly rooted. Courtesy of USGS and Google.

The most likely scenario is that the hogs and the bulrush are locked in an ecological mutualism: bulrush provides the hogs with an abundant food source while the hogs maintain the bulrush patches by periodic rooting that discourages invasion by needlerush and Saw-grass (which are probably competitively dominant to bulrush in their preferred salinities). Thus both species are regulating the other, which may explain the stability of the bulrush patches. At the edges of the bulrush patches, the needlerush is sometimes pushed up as the hogs root the entire patch, likely checking the advance of the needlerush (pers. obs.). Additionally, during this study it was noted that most bulrush rhizomes tended to be in a horizon below 10 cm into the substrate. This may be due to the hogs consuming most of the rhizomes above this level, explaining how bulrush is able to flourish despite heavy feeding by hogs. More work is needed to elucidate the exact nature and extent of this mutualism between an omnivore and its (locally) dominant food.

## **Conclusion**

Feral Hogs are global pests that are extremely destructive to native plants, animals, and ecosystems in general. Much research has been done describing the physical impacts they have through trampling, rooting, and consumption, but the indirect effects they have on the ecosystems through nutrient transport may also be important and should not be ignored. Additionally, when hogs have been present in a system for a long period of time, they may have established novel ecological links that change the structure of the system. While the hog-induced changes may or may not be desirable, studies beyond cataloguing physical damage will give a deeper understanding of the types of impacts that exotics and omnivores have on native communities, and of ecological interactions as a whole.

## CHAPTER 5 DEFINING WILDERNESS

### **Introduction**

The division between Human and Nature is one of the most fundamental distinctions made about the essence of reality (Brown 2007). The existence, exact placement, and character of this Great Divide have implications for the proper role and nature of humanity itself and are therefore matters of longstanding and often heated debate (Callicott 2007; Oelschlaeger 2007). This debate was previously meant to define an objective, naturalistic morality but more recently the primary importance of the Human/Nature division has been to conservation biology (Cronon 1995; Ereshefsky 2007; Oelschlaeger 1991). With this perspective, the focus shifts to the division between human-engineered landscapes (cultural areas) and natural landscapes (wilderness). Thus the discussion revolves around the meanings of the word “wilderness”.

With the globalization of the largely American invention of national parks, came the exportation of the American conception of ‘wilderness’ (Harmon 1987). Because the American ideal of wilderness is a vast uninhabited, roadless, purely natural landscape (Nash 1967), there has been a backlash against the concept of wilderness in general in countries that may have no areas that could qualify as wilderness under this particular definition (due to space or extent of anthropogenic influence) and in countries with populations dependant on the natural landscape (Bayet 1994; Guha 1989). These populations have historically been and are currently still susceptible to being dispossessed of their lands, livelihoods, and eventually social and cultural cohesion when protected areas are gazetted (Goldman 2011). Thus hostility towards past

colonial injustices and suspicion of current 'Green Imperialism' is transferred to the concept of wilderness and sometimes even to conservation in general (Guha 1998). By examining the core philosophical problems with universally applying the dominant Western definition of wilderness, I hope to uncover a basal definition of wilderness that is both philosophically sound and useful in conceptually uniting the conflicting understandings of 'wilderness' found in differing cultures.

### **Defining Wilderness American Style**

The standard legal definition found in the U. S. Wilderness Act (1964) reflects the American cultural ideal, guides land use and the establishment of protected areas within the United States, and, acting as a model for other parts of the world, has ramifications for conservation far beyond its jurisdiction. It states:

A wilderness, in contrast with those areas where man and his own works dominate the landscape, is hereby recognized as an area where the earth and its community of life are untrammelled by man, where man himself is a visitor who does not remain.

This is the core wilderness definition of the Act which further qualifies a legal wilderness with three major points. A wilderness 1) is large,  $\geq 5000$  acres (2023 ha), 2) is natural with little human influence, and 3) has no permanent human presence. These three points are consistent with and often appear in the laws of other countries with large areas of sparsely inhabited wildlands, e.g., Canada: Wilderness and Ecological Reserves Act (1980) and Provincial Parks and Conservation Reserves Act (2006), Australia: NSW Wilderness Act (1987), and Iceland: Nature Conservation Act (1999), and in the International Union for the Conservation of Nature Wilderness Area classification of protected areas (category Ib; Dudley 2008).

These three points resonate with many cultural definitions of wilderness. However, they do not necessarily transfer well into cultures that may have very different economic, spatial, and philosophical relationships with nature and thus very different ideas of what wilderness is. Given that wilderness acts as a sort of Holy Grail (an ideal goal combined with a romantic vision with long history and deep spiritual and emotional meanings) for the conservation movement, American-style wilderness ideals were naturally exported at the same time as American-style conservation science. Unfortunately, the mismatch between ideas of wilderness and practical circumstances on the ground can lead to misunderstandings, mismanagement, and/or the inappropriate establishment of fortress-style conservation and the resulting displacement and disenfranchisement of indigenous populations (Goldman 2011; Guha 1989). Worse, the outright hostility to the American ideal of wilderness and the fear of new-colonialism can develop into an aversion to conservation in general and hamstring international and local conservation efforts (Spinage 1998).

In part to address these problems, many legal definitions of wilderness arbitrarily focus on technological level, traditional use, race/ethnicity, *etc.* For example, the South Australia Wilderness Protection Act (SAWPA) (1992) states that “the land and its ecosystems must not have been affected, or must have been affected to only a minor extent, by modern technology”. However, definitions of wilderness that allow traditional use are plagued with the philosophical problems justifying why certain uses, technologies, or people are compatible with wilderness while others are not.

While new technologies tend to be more effective than traditional ones and thus increase the potential ecological impact of each individual, even the most traditional

technologies are not in and of themselves necessarily sustainable, as witnessed by numerous ancient anthropogenic extinctions (Barnosky et al. 2004) and landscape transformations (Diamond 1994). Even if a particular traditional system has been in place for long periods of time, changing environmental conditions may demand corresponding changes in use to maintain sustainability.

Traditional use by indigenous peoples in the eyes of colonizers and their descendents tends to be whichever indigenous group happened to be in an area doing whatever they were doing at the time of colonization. This view does not allow for change (cultural, spatial, or environmental), and naturally leads to a dogmatic assumption of stability and sustainability. This view is encoded in the SAWPA (1992), which gives a management goal of “restoration of land and its ecosystems to their condition before European colonisation”. Additionally, the assumption of sustainability rests on assumptions of general stability of the number of traditional users and their individual impacts. With environmental conditions, numbers of traditional users, and access to more effective technologies changing, it is clear that any traditional use must be managed in some way; however limiting access to subsistence users presents greater moral and practical difficulties than limiting access to recreational or facultative users.

Adding to the difficulties involved in defining traditional use is the fact that the issue of traditional use often does not revolve around traditional use, or even traditional technologies, it revolves around the ethnicity or race of the traditional *users*. As examples, the SAWPA allows for hunting and observation of traditions by Aboriginals in wilderness areas, the Finnish Act on Wilderness Reserves (1991) states that wilderness

reserves are established in part to preserve Lapp culture, and Dear and Myers (2005) found that the race of the hunter determined whether or not subsistence hunting in Alaskan wilderness was supported for 33% of recreational visitors.

Traditional use, then, is often a compromise between having a human-free wilderness area and social justice for indigenous peoples, which can lead to the shaky conclusion that a blond hunter in Alaska is somehow incompatible with the wildness of a place but an Inuit hunter is not. Likewise, an ethnic German hunter would not be incompatible with Alpine wilderness but a naturalized German hunter born in Lesotho would. The mental contortions involved in philosophically allowing for certain ethnicities or races in wilderness, defined as a place without humans, at best puts a barrier between two groups and at worst belittles a culture and dehumanizes a people. If humans do not live in wilderness, it follows that anyone living in a wilderness is, *ipso facto*, subhuman. This is essentially the line of thought that led to the colonial (and current; (Diegues 1998) idea of *terra nullius* (un- or underdeveloped/uncultivated land is not owned and is therefore free for the taking), which gave colonists a moral excuse, or even imperative, for dispossessing indigenous people of their land (Bayet 1994).

To avoid misunderstandings, defuse conflict, correct prejudices, and facilitate communication, it is necessary to unify in the vast array of wilderness definitions. This cannot be done by replacing a diversity of definitions with uniformity because even the best single definition would be inappropriate in many cultures and contexts. Rather than replacing diversity, it would be better to uncover the fundamental unity upon which the diversity of definitions and opinions are built. If a fundamental and logically sound definition of wilderness unbiased by any particular culture can be established, it can

help make people aware of their own deeply held perceptions and serve as a basis for intercultural communication and understanding about conservation, allowing the concept of conservation to be locally adapted and appreciated more readily.

### **A Basal Definition: The Not-So-Great Divide**

Even in the Western tradition, definitions of 'wilderness' are diverse (Ereshefsky 2007) and run the gamut from excluding all human influence whatsoever, to allowing some types of human influence, to allowing all human influence (because humans are just another natural product of evolution; Henberg 1994). Contrasting with the extreme definitions, which are clear in theory but uselessly encompass either nothing or everything, the practical definitions of wilderness allow a confusing variety of types and extents of human influence (Ereshefsky 2007).

The ultimate problem with attempting an objective definition of 'wilderness', is that it inherently requires a negative definition; not a definition of what it is, but of what it *is not*. Just as it is impossible to define 'dark', 'cold', or 'quiet' without reference to light, heat, or sound, it is impossible to define 'wilderness' without reference to cultural space. Just as dark, cold, and quiet do not require the total lack of light, heat, and sound, wilderness can be defined as the relative lack of cultural influence. The exact placement and width of the boundary between cultural space and wilderness and how much time and effort is needed to transform an area of wilderness into a cultural space will depend on the culture of the observer. However, it is fairly easy to construct a usable and flexible definition of cultural space.

Cultural space is an area in which the biotic community is purposefully and fundamentally altered and that alteration is constantly maintained by humans, for the use of humans and/or their domesticated symbionts. Generally this involves a

significant conscious effort to control and transform land cover and exclude undesirable flora and fauna. Because significant effort is involved, the boundaries of cultural landscapes tend to be surprisingly sharp with an area either maintained or not (Worman 2010). For example, settlements and agricultural land (including improved pasture planted with desirable grasses) are obviously within the cultural sphere. However, a river, polluted beyond recognition, though significantly and continuously altered, is not within the cultural sphere as the alteration was not an intentional endpoint. A grassland, burned to attract game or provide better grazing, is purposefully altered but not maintained so also does not enter into the cultural sphere. A coppiced woodland is also altered but with little maintenance or effort to control. Instead, what effort is expended is focused on management of a few key characteristics of a small subset of species, not purposeful maintenance of a fundamentally different community. Forest clearing, whether done to procure wood or produce rangeland, does not necessarily move an area into the cultural sphere if the subsequent succession proceeds without undue human direction. Low intensity management of certain species or morphotypes, such as periodic burning or clearing of woody species does not transfer an area into the cultural sphere. High intensity management to purposefully control the grass and herb species and access by wildlife, however, would.

It is worth noting the difference between my use of the words “maintenance” and “management”. Here I use the term “maintenance” to mean purposeful, high effort, frequent, and consistent activities meant to preserve a fundamental anthropogenic alteration to the biotic community, and “management” to mean purposeful, low effort, infrequent, and often contingent activities meant to preserve or increase some value of

the biotic community. Clearly there is a continuum between these two terms and, thus, a zone of transition (however narrow or broad) between cultural space and wilderness.

Defining wilderness as any area outside human cultural space avoids several of the problems inherent to other definitions (Ereshefsky 2007). It avoids the futility of the extreme definitions and the arbitrariness of the others. This definition allows for human use of wilderness (whether recreational or subsistence) and, perhaps most importantly, is largely decoupled from spatial considerations. Many definitions of wilderness explicitly or implicitly focus on size as a major criterion, and for good reasons: larger areas tend to be more sublime, more biologically diverse, more ecologically complete and stable, more dangerous, and with more opportunities for solitude; thus, more wild. Leopold (1921) defines a wilderness as being large enough for a two week packing trip and many official definitions include minimum sizes for wilderness areas (2023 ha, Wilderness Act 1964; 2500 ha, Nature Conservation Act 1999), state that wildernesses are large areas (Wilderness and Ecological Reserves Act 1980; Provincial Parks and Conservation Reserves Act 2006; Dudley 2008), or imply large areas by the scale of established wildernesses (15,000-294,000 ha; Act on Wilderness Reserves 1991).

Implicit to scale is the generally unspoken issue of continuity. Wildernesses are seen as areas that are entire landscapes uninterrupted and unfragmented by human works. Of course, there is a multitude of practical reasons to stress continuity, including ecosystem sensitivity to fragmentation and ease of management. However, by focusing on continuity and entire landscapes, the official and unofficial interpretations of “wilderness” from the Western world may not be readily transferable to other parts of the globe where only small areas remain wild or human populations are integrated into a

largely natural landscape. Focusing on landscape-scale wilderness conservation can lead to lost opportunities for gazetted protected areas, the barring of local people from accessing important resources, or the relocation of entire communities. Fears of these externally applied social upheavals can lead to an anti-conservation backlash from people who would likely otherwise support conservation (Goldman 2011).

By defining “wilderness” as a non-cultural area, the concept of wilderness becomes independent of size and continuity. Wilderness then relates to wilderness as water relates to a body of water regardless of size and shape. Just as bodies of water vary from huge and contiguous (oceans) to small (prairie potholes) with complex boundaries (rivers and streams) wilderness is not limited to vast uninterrupted wild tracts but is instead an area of wilderness whether large and contiguous with simple boundaries or small with complex boundaries enclosing or interdigitated with cultural areas. Thus, under this definition, a landscape can contain both wilderness and cultural lands and small cultural areas do not need to be forced under the spatial and philosophical umbrella of wilderness.

Yet the question remains: why are the cultural spaces of humans considered so fundamentally different from the living spaces engineered by other organisms like beaver ponds or termite mounds? Implicit to all definitions of wilderness is the tenet that humans are the only force able to destroy wilderness (Ereshefsky 2007). Even those that focus on ecosystem qualities, such as intact ecosystem functions or diversity, are still based on the assumption that relevant disruptions of the ecosystem qualities are anthropogenic. A volcano covering a forest with lava is seen as fundamentally different from humans paving a parking lot.

Callicott (2007) makes the case for the Great Divide being based in the differing temporal scales of evolution and culture. Cultural changes are orders of magnitude faster than geological, climactic, or evolutionary changes, and land transformations initiated by human cultures cannot be adapted to as quickly as they change. This perspective is largely true, and certainly important when considering anthropogenic impacts, however, even non-anthropogenic changes can occur at super-evolutionary speeds. Quick geologic changes, such as volcanic eruptions, landslides, meteors, unusual floods or draining events, are thankfully rare and one-time events. On the other hand, non-anthropogenic biological invasions can have rapid and persistent impacts on the native communities just like human-mediated invasions and anthropogenic landscape transformation. Additionally, the temporal mismatch explanation is a *post hoc* justification requiring modern science to explain a concept that seems to have been shared by all human cultures (see below).

Modern biology, while obliterating past beliefs about the special creation of Human as apart, above, and fundamentally different from Nature, seems to tacitly support such a division by focusing much of ecology and conservation biology on the biotic world *sans* humans (*i.e.*, wilderness). The answer to this apparent conundrum lies in the matter of perception. Scientists, and every other human, view the world from an anthropocentric perspective. This statement is not meant to be pejorative and is certainly made with the human capability of empathy in mind, but just as individual humans have a sense of self and others, humans collectively look outwards from themselves and their cultural space at the Other, the Wilderness. If perspective is shifted from anthropocentric to, for example, castoracentric, it is easy to see how the

concept of wilderness also shifts. The lodge, dam, canals, and dam-created pond are the beaver's engineered space (an acultural equivalent to cultural space). Outside of this area is the castoracentric wilderness. The wooded land around the pond is utilized for food and materiel but is not transformed and maintained in the way that the engineered space is and remains a place of relative vulnerability and danger. The concept of wilderness need not divide Human from Nature because every species that creates engineered space, however small and temporary, separates an area from the whole and in doing so, creates its own version of wilderness.

Of course, humans are primarily concerned with the anthropocentric version of wilderness and anthropogenic impacts on wilderness. This is why deforestation caused by beaver ponds is seen as fundamentally different from anthropogenic deforestation. Simply put, humans are concerned with human presence in and impacts on anthropocentric wilderness both through a sense of responsibility and because it would be difficult if not unnatural to view the world any other way. The extent and magnitude of anthropogenic alteration of the biosphere are just two of the qualities that make humans a particularly notable and important member of Earth's biotic community especially in terms of preserving biodiversity, but they in no way separate or remove humans from that community. Thus the definition of wilderness as the space outside the engineered space of a species solves an age-old philosophical conundrum by recognizing that the Great Divide is simply a identity boundary possessed by every species dividing it and its engineered space (if any) from the rest of the biosphere.

### **Universality of the Basal Definition**

For this definition of wilderness to be of pancultural use for discussions of conservation, the distinction between human engineered (or cultural) space and extra-

cultural space (here termed 'wilderness') must already be recognized in some way by most if not all peoples. This position is likely to be a controversial one as the idea that every human culture contains some sort of wilderness concept defies long- and fondly-held paradigms that focus on differences in amount of material culture between peoples. These paradigms include both the outdated that attempt to place certain other cultures on the other side of the Great Divide (such as the paradigms of colonial Europe, which often viewed conquered peoples as sub-human or different biological species altogether) and the more current paradigms that view present ecological problems as symptoms of too much emphasis on the Great Divide and loss of connection with the wilderness. However true or not the latter may be, denying that other peoples recognize cultural space as distinct from everything else (wilderness) is a variant of the Noble Savage idea that civilization is the cause of all human woes and somewhere there is a group of people who live happy fulfilling lives of peace and harmony because they are one with Nature, or at the very least that it is possible to cure human ills by living as one with Nature.

It is of course impossible to positively establish that all human cultures have had a wilderness concept, but any creation and maintenance of cultural space necessitates a recognition of the boundaries of the cultural space and thus a recognition of the division between the cultural space and everything else. Whether the cultural space is a permanent cement-clad city surrounded by intensively used and clearly demarcated agricultural fields, or a group of temporary grass huts in a clearing, the area must be recognized as something different, something more humanized than everything else. Otherwise, there would be no reason to create and maintain it in the first place. Both an

awareness of self and self works (in terms of individuals and as a species) and an evolutionary advantage in being able to recognize the works (and therefore cultural areas) of unknown humans (Dawkins 2006) imply a universal human notion of wilderness. While it is not feasible to review the wilderness concept in every human culture, a review of some will help illustrate the diversity of its expression among cultures. Some authors reviewed here explicitly discuss cultural concepts of wilderness or the Great Divide, others imply a wilderness concept, and one denies the existence of a wilderness concept in his culture.

Attitudes and emotions towards wilderness can vary widely among cultures, individuals, and time periods, and even the distinctness of the division between Human and Nature can vary from being culturally explicit and celebrated to a division that is purposefully minimized (see below). Even the belief that humans are one with Nature or part of the natural world does not eliminate the distinction between self and other and cultural space and wilderness. This phenomenon can be seen quite clearly in modern Western cultures where the belief in a deep and fundamentally important Great Divide exists in spite of the knowledge that humans are simply a naked, bipedal, super-intelligent chimpanzee with genetic and evolutionary kinship with the rest of life and completely dependent on it for survival.

In spite of the differences in attitudes and emotions towards wilderness and differences in emphasis placed on its boundary with cultural space, concepts of wilderness in diverse cultures are unified by certain basic perceptions and spatial organizations. Because wilderness is the constant antithesis to cultural space, a concept of wilderness can be recognized in other cultures by perceived qualities of

danger, chaos, isolation, and/or foreignness that oppose the qualities of relative safety, control, community, and/or belonging that characterize cultural spaces (Worman 2010). Additionally, cultural areas, especially small ones, tend to be centralized with relatively simple, often distinctly demarcated, boundaries with the wilderness (see below).

Lee's (1993) study of the Ju/'hoansi, a Khoi-San group of hunters and gatherers in southern Africa, explicitly illustrates a detailed civilization/wilderness boundary (p. 35). The village (*chu/o*) as the cultural space means "safety, comfort and companionship" to the Ju/'hoansi, while the bush (*t'si*) is the wilderness (p. 31). The Ju/'hoansi camps are described as a series of concentric zones with unique characters and uses: the central plaza, the ring of huts and firepits, a zone of middens behind the huts, a larger zone for butchering and cooking of larger animals, a buffer zone, and an area for defecation. Beyond these is the *t'si* (bush), the wilderness. The foundational definition of wilderness presented in the current paper would count only the plaza and huts as cultural space as these spaces are maintained clear of grass and brush. The Ju/'hoansi vision of cultural space seems to add the middens, butchering zone, buffer zone and defecation zone as well. As hunters and gatherers, the Ju/'hoansi have an intimate knowledge of and are comfortable in the *t'si*, but they have no great love or spiritual reverence for the wilderness (p. 31).

In Turnbull's (1961) study of another group of hunters and gatherers, the Mbuti Pygmies of central Africa, he does not specifically address the existence of a Great Divide and many comments made both by Turnbull and the Bambuti seem to indicate a lack of a wilderness concept. For instance, Turnbull mentions many times that the Bambuti view the forest as their home and are completely comfortable in it (pp. 13-14,

55, 172). He stresses their faith in the fundamental goodness of the forest (pp. 92-93) and even goes so far as to say, "They have no fear, because for them there is no danger [in the forest]," (p. 14). One of the Bambuti expressed similar sentiments: "The forest is father and mother to us,' he said, 'and like a father or mother it gives us everything we need—food, clothing, shelter, warmth... and affection,'" (p. 92).

Yet the conclusion that the Bambuti lack a wilderness concept would be premature. The typical arrangement of huts in a village is a "close little circle" (p. 45) and examples given of "things going wrong" in their world are army ants or leopards that "come in" or "invade" the camp (p. 92), both of which indicate the solidarity of cultural space separated from the forest. More telling is a Mumbuti's description of the punishment for incest:

'He has been driven to the forest,' he said, 'and he will have to live there alone. Nobody will accept him into their group after what he has done. And he will die, because one cannot live alone in the forest. The forest will kill him,' (p. 112).

Thus, while the Bambuti have affection and reverence for the forest, they also recognize the division between society and wilderness. Turnbull's focus on the affection should be taken in the context of his contrasting the Bambuti-forest relationship with the distaste the Bambuti hold for the Bantu villages (pp. 172, 227) and the horrible fear and hatred the neighbouring Bantu tribes have for the forest they view as hostile and evil (p. 55). The Bantu agriculturalists are described as having perceptions of the forest that are easily recognizable as a wilderness concept. The forest is seen as foreign, rarely visited, constantly fought, and filled with dangerous spirits and animals (pp. 13, 171). Thus while both peoples view the forest as wilderness, their emotions regarding and perceptions of the wilderness are polar opposites.

Chagnon (1992) states that the Yānomamö, a hunting/gathering/horticultural people of South America, have a very explicit and prideful Great Divide based on the possession of culture by humans. They divide the world into *urihi tä rimö* (things of the forest) and *yahi tä rimö* (things of the village) (p. 105), the latter of which also includes gardens (p. 55). Although quite knowledgeable and skilled in the forest, the Yānomamö children have a safety limit around the villages beyond which they are not allowed (Plotkin 1993, p. 252) and the adults have an abject fear of being caught in the forest at night without fire due to the dangers presented by malevolent ghosts (*bore*) and jaguars (Chagnon 1992, pp. 106 & 113).

The Naxi people from southwestern China describe the Great Divide as having occurred when the Naxi progenitor and his brother Shu, the Nature governing spirit, went their separate ways with Naxi taking the valleys, crops, and domestic animals and Shu taking the mountains, rivers, forests, birds, and wild animals (Xu et al. 2005).

Some cultures physically delineate the boundary between cultural space and wilderness. For example, the Tibetans divide the world into internal space (the villages and fields) and external space (the mountains and forests) with the boundary marked with stone piles (*mani*) and incense burners (Litzinger 2004). Likewise, the Hani from Southeast Asia build a gate (*lanlkang*) to separate the village (*pucang*; *pu* = village, *cang* = place or forest) from the nonhuman world (*baolcang*). Interestingly, the villages are surrounded by protective forests hundreds of meters wide that are also called *pucang* (Xu et al. 2005), which seems to indicate that the protective forest is incorporated into the cultural space or at least considered transitional between the cultural space and wilderness.

In Standing Bear's (1933) autoethnography he states that wilderness was a European idea that was completely foreign to the Sioux. His claim has been repeated and used as a criticism of the concept of wilderness (Callicott & Nelson 1998; Nash 1967, 4<sup>th</sup> ed. p. xiii), however it is more correctly interpreted as a criticism of the contemporaneous Euro-American perception of wilderness. Standing Bear's depiction of his childhood in relatively intact Siouan culture is both highly idealized, elegiac, and purposefully contrasted with that of the Euro-Americans. It must be understood that his writing is more literary than literal and with a strong social agenda. (This is made clear by comparing Standing Bear's idyllic depiction of Siouan culture with an anthropological one; e.g., Hassrick 1964.)

Did Standing Bear gloss over the Lakota perception of wilderness? While the unity of all things is stressed in Lakota cosmology, the division between human and non-human is important (DeMallie 1987). Indeed, the Lakota do have the concept of cohesive cultural space as separate from wilderness. The solidarity of cultural space is evidenced by the prototypical layout of a village (the actual layout of which was often dependent on topography and obstacles; Hassrick 1964, p.173-174): the tipis arranged in a circle around a central plaza (*hocoka*) with an opening in the circle for the official entrance (*oinapa*) with sweat lodges (*ini tipi*) outside the circle (Walker 1982, pp. 21-23). The limits of cultural space were socially significant as people setting up tipis away from the main camp were establishing a different camp with different governance (Walker 1982, pp. 23-25).

More telling is that Lakota does have words for wilderness: *makoskan* (a place where no one dwells, treeless, or desert; possibly with the connotation of "being in

vain”) and *tiwokitahena* (being away from houses, homeless) (Buechel & Manhart 2002). Thus, Standing Bear’s (1933) apparent rejection of the wilderness concept was actually only a rejection of the dominant Euro-American perception of wilderness at the time: “...land ‘infested’ with ‘wild’ animals and ‘savage’ people,” (p. 38). Furthermore, numerous native examples of the wilderness concept from North, Central, and South America (Bierhorst 1994, pp. 140-155), should be enough to dispel the myth that American Indians lacked a concept of wilderness (Rolston 1991).

### **Caveats and Conclusions**

One strength of the definition of wilderness presented here is that it is flexible enough to act as a uniform foundation through which cultural variations can begin to be understood. It does not define temporal or spatial limits of wilderness. Thus it leaves many questions for different cultures to answer differently. It may be clear that land ploughed and farmed every year is maintained in cultural space, but if abandoned, how long before it leaves cultural space and becomes wilderness? By this basic definition, abandoned land would immediately leave cultural space and enter into wilderness, but different cultures likely have different time frames. In some cultures the transition may be immediate and in others take a few years or even a few centuries. In the interim, the land may be considered to be in a sort of an “old field” limbo perhaps similar to cemeteries (which are cultural areas but not the realm of the living; (Bierhorst 1994, p. 145).

Compounded difficulty comes from not abandoning the land but letting it lie fallow. Do future plans to reuse land affect the perception of its time to return to wilderness? If three years (for example) is enough for a return to wilderness once abandoned, is a field left fallow for four years also considered wilderness? While the answer will vary

from culture to culture, it does however seem likely that typical fallow periods would be shorter than the required return time to wilderness for any particular culture.

In other cases, a tree crop may be planted but not maintained or destroyed until harvest if at all. If five years (for example) is enough for an abandoned plot to return to wilderness, does a 20 year rotation in pine harvest mean that an area of silviculture becomes a wilderness at some point before harvest if not maintained in any way? For example, a forest full of even-aged monocultures is considered a type of wilderness by Germans (Imort 2005) but a tree farm by others (O'Hara 2001).

It is clear that under this definition of wilderness, which does not consider size, age, fragmentation, and disturbance, that all wilderness areas are not equivalent. They may differ in biome/ecosystem type, level of wildness, biotic and conservation value, and cultural categorization (Table 5-1), all of which must be taken into consideration when establishing conservation plans.

Table 5-1. Examples of cultural wilderness categories

Category	Explanation	Example	Culture/Location	Sources
Archetypical	One habitat type acting as an ideal cultural image of wilderness	Forests	Germany	(Worman 2010)
		Mountains	Korea	(Worman 2010)
No-man's-lands	Buffer zones between hostile peoples	Great Prussian Wilderness	Teutonic Knights, Lithuanians, Poles	(van Vuure 2005)
		Demilitarized Zone	Korea	(Kim 1997)
Sacred lands	Places with religious or spiritual meaning	Rwenzori peaks	Bukonzo, Uganda	(Stacey 2003)
		Sacred groves	Western Ghats, India	(Gadgil & Vartak 1976)
		Holy hills	Dai	(Xu et al. 2005)
Wastelands	Areas with little or no value esp. for development	Badlands National Park	South Dakota	
		Savannas	Tiriós	(Plotkin 1993)

This basal definition of wilderness can be constructively used even in the most disturbed regions because it embraces most of the landscapes in which conservationists are generally interested: everything from pristine natural to highly disturbed quasi-natural ecosystems, from candidates for preservation to candidates for restoration. However, like other wilderness definitions, the one proposed here cannot define most conservation goals. Goals such as ecosystem representation, function, productivity, native diversity, stability, evolvability, or preservation of a scientific baseline are not necessarily informed by any wilderness concept and some can be pursued at least partly in cultural areas. However, given that land use decisions appear to be influenced by cultural definitions of wilderness (Worman 2010), it would be surprising if conservation decisions were not likewise influenced, even if ostensibly purely scientific and rational. Thus knowledge of one's own cultural biases and idiosyncrasies may help cross-cultural conservationists put them aside when they are out of place and use more culturally appropriate wilderness definitions. Using local interpretations of wilderness may help communicate the more easily verbalized scientific and practical benefits on a deeper emotional level. Additionally, conservation goals that explicitly include aesthetics and recreation do need to be informed by local and/or external wilderness ideals (depending on the targeted group).

A common foundational starting point may facilitate the creation and explanation of both scientific and aesthetic goals that are acceptable to multiple groups, allowing conservation to be tailored to local cultures and conditions. Locally adapting conservation initiatives to give more cultural and intellectual ownership to the people directly affected by them will likely encourage local support for and the ultimate success

of the initiatives and should not be minimized or overlooked (Lepp & Holland 2006).

Additionally, the concept of wilderness appearing to be culturally universal signals that 'wilderness' is integral to human cosmologies and therefore the continued existence of wilderness is an assumed part of human world views. Conservation is simply an active extension and defence of that assumption.

## CHAPTER 6 TROOPING FAIRIES, TROLLS, AND TALKING TIGERS: THE INFLUENCE OF TRADITIONAL WILDERNESS ARCHETYPES ON CURRENT LAND USE PATTERNS

### **Introduction**

Wilderness is the landscape on the other side of the Great Divide that separates Human from Nature (Nash 1967; Oelschlaeger 1991). It is the polar opposite of civilization, yet as the ever-present Otherness, it plays a diversity of important roles within human cultures, including spiritual, psychological, mythical, and economic (Nash 1967). Because of these significant roles, the concept of “wilderness” has been the subject of frequent debates (Callicott 2007; Callicott & Nelson 1998; Ereshefsky 2007; Nelson & Callicott 2008), made more contentious by the cultural, subcultural, and individual subjectivity of the rational and emotional perceptions and interpretations of wilderness (Nash 1967). Here I explore the idea that different cultures have different wilderness archetypes (a habitat that represents the ultimate or ideal wilderness to a culture) due to different external and internal forces, which may result in differing landscape use patterns and differing conservation priorities, concerns, and opportunities (Figure 6-1).

An inspection of the spiritual meanings of wilderness can provide an example of how diverse and flexible views of wilderness can be. In some cultures (*e.g.*, East Asian, Nash 1967; Zaramo Bantus, Sunseri 2005; and Mbuti Pygmies, Turnbull 1961) wilderness has traditionally been viewed as being a place of spirituality and holiness (though not necessarily free of spiritual danger), whereas in others, (*e.g.*, medieval European, ancient Hebrew, and early American; Nash 1967) wilderness was seen as

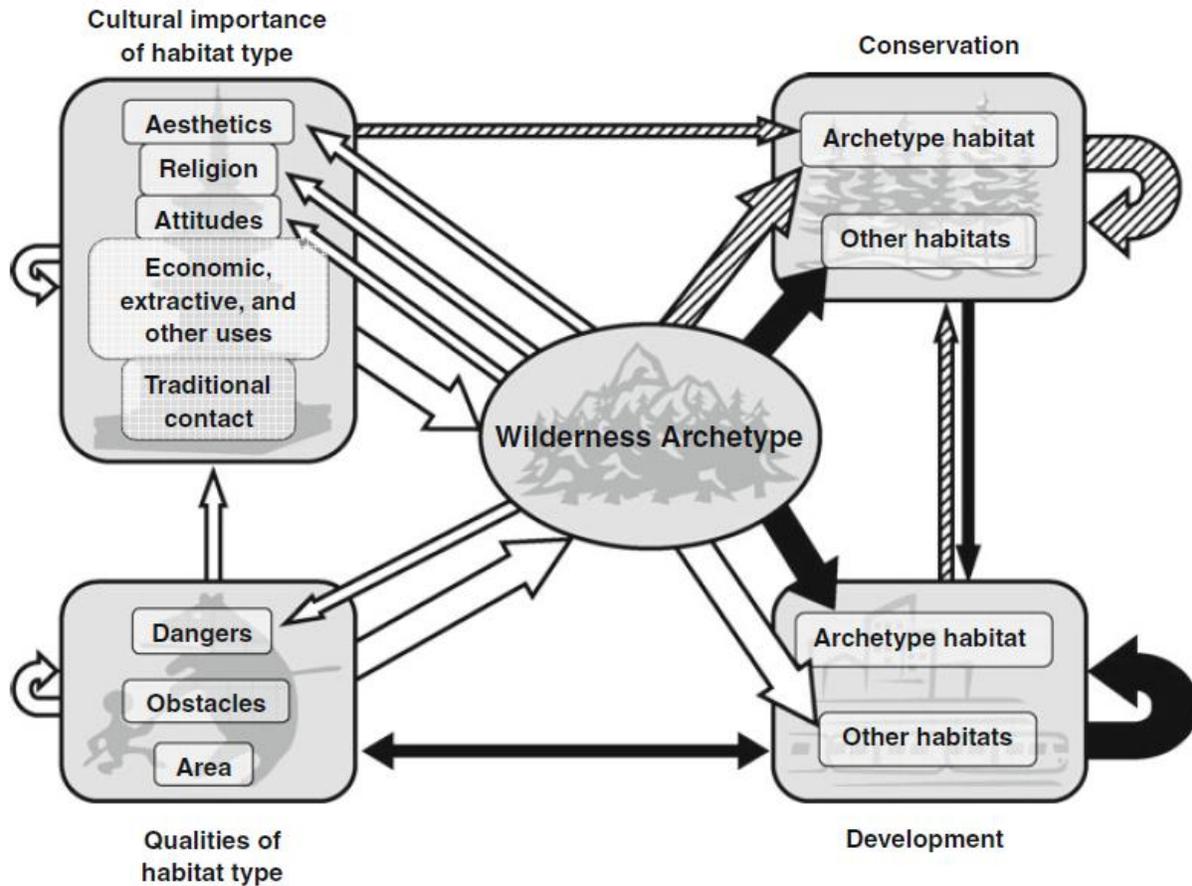


Figure 6-1. The functional relationships among a wilderness archetype and the cultural and natural qualities that influence and are influenced by it. Only relationships discussed in the paper are included for simplicity. The color of the arrows indicates the typical nature of the interactions: white = positive, black = negative, cross-hatched = positive and/or negative or more complex depending on the situation. For example, conservation has a limiting influence on development, but development has a complex influence on conservation (development destroys habitats but by increasing the rarity of a habitat, makes conservation efforts more likely). Thick arrows indicate connections that are major themes dealt with in this paper. Thin arrows indicate connections that have minor mentions in this paper. The thicknesses of the arrows *do not* indicate strength or importance of the relationships.

being profane and evil. Additionally, a culture's views of wilderness are not static. For example, the dominant European/American view of wilderness shifted from largely fearful and hostile (pre-Romantic), to idealized and sublime (Romantic), to recreational

and ecological (Modern) (Imort 2005; Nash 1967). A diversity of views can also exist within a single culture at one point in time because of differences among subcultures and individuals (Nash 1967; Ross-Bryant 2005). However, because of the coexistence of both negative qualities (dangers and isolation) and positive qualities (economic value and relief from the evils of society) inherent in wildernesses, any perception of wilderness is likely to be complex.

In addition to the varied emotional and intellectual responses to wildernesses, the habitat that represents the physical ideal, or archetype, of wilderness also varies among cultures. For example, the ancient Hebrew desert wilderness archetype contrasts with the central European forest archetype (Nash 1967) and the bush wilderness archetypes found among various peoples of the savanna/scrub regions of Southern and East Africa (Lee 1993; Burnett & wa Kang'ethe 1994). These wilderness archetypes are clearly based upon the dominant natural land cover in each area, but can likely be modified by a culture's use and interface with each habitat. In a complex world where even the simplest landscape has a diversity of habitats, and cultures come into contact with multiple landscapes, interpretations of wilderness archetypes are probably also influenced by the negative qualities of each habitat type such as relative hostility (including dangers like large predators, diseases, and other people), resistance to development, and difficulty of travel. Religion, history, and amount of contact with and use of different habitat types are also likely to influence a culture's wilderness archetype. Additionally, habitat complexity promotes a multiplicity of interpretations: is a forested mountain a mountain or a forest? Is a swamp a forest or a wetland?

In spite of a diversity of views and archetypes, some generalizations can be made about wilderness. Wilderness can be defined as any area that is outside the cultural sphere and therefore relatively free from the conscious high intensity maintenance to which the biotic communities within the cultural sphere are subjected (Chapter 5). Thusly defined, wilderness is a very broad category that includes areas from the large, pristine, primordial ideal of wilderness to small-scale, heavily disturbed secondary growth. Although the range of economic activities that take place in wilderness and the importance of each naturally varies among economies and cultures, wilderness generally provides direct material economic value through wood/fuel cutting, hunting, fishing, gathering of medicinal, edible, or useful plants and fungi, foraging by domesticated animals, gathering wild honey, *etc.* Thus the relationships between wilderness and human societies tend to be extractive and even at times managerial but typically with limited input and control by the people.

The positive values provided by wildernesses are mitigated by their real and perceived dangers (including wild animals, dangerous people, malevolent spirits, lack of assistance in an emergency, disease, *etc.*; Blackbourn 2004; Gudermann 2005; Imort 2005; Nash 1967), which of course vary with location and culture. Additionally, because wildernesses are outside the cultural sphere and contain relatively few and mostly transient users, physical and psychological social controls are weak or absent (Nash 1967). Hence wildernesses assume another role as havens for people rejected by, ejected from, or otherwise escaping from society (*e.g.*, thieves, murderers, witches, persecuted groups, vagabonds, *etc.*; Blackbourn 2004; Radkau 2005; Sunseri 2005). So, although uses of wilderness are many and normal, individuals who spend too much

time in the wilderness away from respectable society are potentially viewed with suspicion. This situation presents a serious risk of ostracism or scapegoating and likely synergizes with the more obvious dangers of wilderness in discouraging people from venturing too far from civilization when settling. The perception of dangers (both real and imagined), and thus the avoidance of wilderness, is likely to be especially strong for archetypal wildernesses lending them a heightened level of protection from and resistance to development. This reluctance to develop archetypes on the part of individuals or governments need not be conscious or entirely rational given the strong emotions elicited by wildernesses and the importance of emotions in ostensibly rational cost-benefit decisions (Bechara 2004).

If cultural archetypes of wilderness vary and archetypal wilderness areas are somewhat protected by the perception of their wildness, cultures with different wilderness archetypes might create culturally distinctive land use patterns reflecting their wilderness archetypes (operating in concert with topographical, geological, and ecological considerations). Differences in patterns are likely most easily seen between cultures with wilderness archetypes defined by topography and those defined by land cover, because terrain is much more resistant to change than land cover and therefore more likely to successfully check development. The hypothesis that the land use patterns of cultures vary predictably with their respective wilderness archetypes is here examined by first attempting to distill wilderness archetypes from the folktales of three cultures. Then, for the cultures with identifiable wilderness archetypes, the ruggedness of the cultural areas was compared with that of the wilderness areas within and between cultures. Additionally, elevational cross sections of the cultural-wilderness boundary

were compared between cultures. Cultures with topographically defined wilderness archetypes should have stricter tolerances for ruggedness in developed areas as well as civilization/wilderness transitions that have more predictable and consistent elevational cross sections.

## **Methods**

### **Wilderness Archetypes**

To establish the cultural archetypes of wilderness, wilderness descriptions were gleaned from the folklore of three cultures: German, Irish, and Korean (see next section). These archetypes were then compared with wilderness types contained in the names of modern protected areas in each nation to establish the continuity and influence of the traditional archetypes. Though influenced by many other considerations, the naming of protected areas likely gives insight into how the areas are perceived by the managers and how they are intended to be perceived by the public, and thus should be biased towards cultural archetypes of wilderness. The three cultures were chosen due to the availability of folklore, as well as an *a priori* expectation that the wilderness archetypes of these cultures differed.

The possible terrain/habitat categories (cliff/canyon, forest, island, marine/coastal, meadow, mountain, river/lake, rock/cave, scrub, stream/pond, valley, and wetland) were defined by the data. The “mountain” category is broad and includes hills, plateaus, moraines, and other highlands, as well as more distinctly montane terrain such as summits, peaks, *etc.* This choice was driven by the broad use of the Korean word “*san*” (mountain), which is used more inclusively than its English counterpart and is applied to relatively small hills as well as rocky summits (pers. obs.). This linguistic difference likely reflects a difference in cultural perceptions. Thus the mountain category of Ireland

and Germany is more inclusive than it would be otherwise, biasing their data towards mountain wilderness archetypes. Some geographical references were counted as multiple geographical types for both the folktales and the protected areas (e.g., “swamp” is both a forest and a wetland).

### **Folk tales**

The Zipes (2003) translation of Grimms’ fairytales was used to establish the traditional German wilderness archetype. Data for the Irish archetype were taken from Yeats (1892) and Curtin (Curtin 1890). Korean folktales were gathered from Zöng (1982) and Ha (1969). Wildernesses were defined as non-anthropogenic places where something dangerous, magical, or supernatural happened to a human protagonist. In the cases that involve a structure that is clearly anthropogenic (whether magical: a candy house, or not: an abandoned cabin) but embedded in and isolated by a natural landscape, the natural landscape was considered a wilderness. To control for story length, each story only counted once for each wilderness type found therein. Stories that were clearly duplicates were only represented by the most complete version.

### **Protected areas**

Wilderness types were gathered from protected areas that were intra-national (e.g., Biosphere Reserves were excluded), ecologically nonspecific (e.g., Marine Protected Areas in South Korea were excluded), and not primarily for single taxon conservation (e.g., North Korean National Monuments and Protected Sites in Ireland were excluded). Protected areas were limited to the national/federal and provincial/state levels to produce data sets comparable in size to those of the folktales (Table 6-1).

Table 6-1. The total number of folk tales and protected areas used from each nation with the number of wildernesses occurring in the folktales and terrain/habitat references in the protected area names.

		Germany	Ireland	Korea
Folk tales	<i>Total stories</i>	279	104	212
	<i>Wildernesses</i>	125	61	63
Protected areas	<i>Total names</i>	113	120	68
	<i>Terrain/Habitat</i>	88	117	62

Protected area names in Germany were taken from the *Bundesamt für Naturschutz* website (the German Federal Nature Conservation Agency; [www.bfn.de](http://www.bfn.de); accessed May, 2009). National Parks and Nature Parks were used for Germany.

Protected area names in Ireland were taken from the websites of *tSeirbhís Páirceanna Náisiúnta agus Fiadhúlra* (the Irish National Parks and Wildlife Service; [www.npws.ie](http://www.npws.ie); accessed May, 2009) and the Northern Ireland Environment Agency ([www.ni-environment.gov.uk](http://www.ni-environment.gov.uk); accessed May, 2009). National Parks and Nature Reserves were used for Ireland and National Nature Reserves for Northern Ireland.

Protected area names for both North and South Korea were taken from the World Database on Protected Areas ([www.wdpa.org](http://www.wdpa.org); accessed May, 2009) augmented with South Korean Provincial Parks from Park *et al.* (2000). National Park names were checked against the *Guknipgong-weon Seobiseu* website (Korean National Park Service; <http://english.knps.or.kr/>; accessed September, 2009). National Parks, Nature Reserves, and Provincial Parks were used for South Korea. National Parks, Natural Reserves, Protected Areas, and Scenery Reserves were used for North Korea.

Both embedded and isolated geographical references in protected area names were counted (e.g., **Glendalough** and Correl **Glen**) due to the synthetic structure of the names (especially in German and Korean). In contrast to the methods used for the

folktales, protected area names with repeated terrain/habitat references were allowed to count more than once in the same category (e.g., Stromberg-Heuchelberg or Slieve Bloom Mountains; “slieve” is an Anglicization of “*sliabh*”, or “mountain”). Ambiguous geographical references (e.g., “*lough*” can mean either “lake” or “fjord”) were clarified using descriptions of the protected areas given by the respective government website and satellite imagery ([www.wpda.org](http://www.wpda.org)).

### **Analysis**

To determine if dominant wilderness archetypes exist in each of the three cultures (*i.e.*, if mentions of a particular wilderness type were unusually common), the data sets were examined for outliers using Peirce’s criterion (Ross 2003). If none were found, the wilderness mentions in folk tales were compared with those in protected area names using Pearson’s correlation as the remaining data sets were normally distributed.

### **Land Use Patterns**

To address the hypothesis that patterns of land use co-vary with wilderness archetypes, elevational data gathered from Google Earth 5.1 (available from <http://earth.google.com/>) were transformed into a ruggedness index (RI) to compare the irregularity of the civilized and wilderness landscapes of the nations with clear wilderness archetypes (Germany and Korea). To reduce the differences in overall topography of the two countries, only mountainous areas in Germany were used. Six mountainous German areas were delineated: Rothaargebirge, Harz, the Odenwald-Spessart-Rhon-Thuringian complex, the Black Forest, the Bavarian Forest Mountains, and the Northern Limestone Alps (Figure AC-1). Elevational transects perpendicular to wilderness-civilization boundaries were also compared.

Government influences land use patterns and intranational cultural differences exist in both Korea and Germany (Ch'oe 2000; Chaney 2005). This is simpler in Korea where traditional cultural differences and current political differences occur between the north and the south; however, preliminary analysis showed there to be no significant differences between either the civilized or wilderness ruggedness indices between North and South Korea. Thus, although different or more detailed methods may show differences between the two, for the purposes of this study, North and South Korea were unified.

To avoid potential biases stemming from current agricultural differences, the same metrics were applied to city areas hemmed in by mountains. However, because there are no large German cities in mountainous areas, the five largest urban areas in Korea (Seoul-Incheon, Busan, Daegu, Gwangju, and Daejeon; Cox 2008) were compared with Sao Paulo, Mexico City, Los Angeles, Istanbul, and Rio de Janeiro, the five largest urban areas hemmed in by mountains in the rest of the world (Cox 2008) excluding Japan and China as they are culturally similar to Korea.

The sampling of the urban areas included the areas of contiguous urban development and the surrounding and included areas of wilderness (Figure AC-2). The sampling area delineation generally followed the ridgeline nearest to the urban development while excluding agricultural land and non-contiguous urban areas and keeping the delineation as simple as possible. Small areas of agricultural land still included were not sampled.

### **Ruggedness index**

The RI was based on a hexagonal plot with 7 elevation-sampling points (the center and the 6 corners), creating 12 equidistant neighbor relationships. The absolute values

of the differences in elevation between neighboring points were summed to create the index. Random locations were sampled until 50 civilized plots and 50 wilderness plots were accumulated. Plots were excluded if the land use was not easily defined (e.g., obscured by cloud cover or low photographic resolution). Plots were considered to be “civilized” if they contained only intensively human maintained landscapes (settlement, crop fields, improved pasture, orchards, *etc.*), but were considered to be “wilderness” if they were not intensively maintained (natural and managed forests, meadows, grasslands, wetlands, *etc.*). Korean tombs, which are generally scattered individually in forested mountains and consciously placed in wilderness, were allowed in wilderness plots. Though Korean Buddhist temples are also purposely placed in the wilderness, they are significant human structures (often with accompanying gardens) and, like hunting cabins, can be hard to distinguish from homes. Thus wilderness plots with any buildings or mines (which can alter the topography) were excluded. Roads and watercourses, along with their rights-of-ways and narrow riparian zones, were allowed in either type of plot because of their linear nature and their presence in both types of landscapes. Plots encompassing both types of landscapes were considered “mixed” and not used for analysis.

Three spatial scales were examined: 250 m, 125 m, and 25 m hexagons (opposite corner to corner distances). These scales run from the scale of villages down to the scale of individual houses. The same center points were used for each of the scales. However as the plot size decreased, mixed plots shifted into the civilized or wilderness category and sampling was ceased once 50 civilized and 50 wilderness plots were measured. For the urban comparisons, only the 125 m scale was used. This scale was

small enough to sample the limited islands of wilderness in the urban areas and also most clearly showed land use differences.

Logistic regressions were applied to the RI profiles to examine the application of land use decision rules. Inverse predictions were made to determine the ruggedness indices corresponding to 5%, 50%, and 95% probabilities of being civilized. 95% confidence intervals (CI's) for the inverse predictions were established using Fieller's (1954) method and compared between the German and Korean predictions at each scale. However, some civilization-wilderness transitions were so sharp that CI's for the inverse predictions could not be established. In these cases, the inverse predictions were directly compared to the other nation's 95% CI's. For the urban comparisons, the 50% inverse predictions and the ranges between the 5% and 95% inverse predictions were compared with *t*-tests. It is expected that cultures with topographic-based wilderness archetypes will have better fitted logistical regressions (higher  $-\log$  likelihood differences from the null, higher  $r^2$ , and greater areas under the Receiver Operating Characteristic (ROC) curves), lower 50% inverse predictions, and a smaller spread between the 95% and 5% inverse predictions than cultures with land cover-based wilderness archetypes. However, as rugged topography has practical ramifications for all human activities, ruggedness should remain an important predictor of civilization across all cultures.

### **Border transects**

To establish the characteristic topography of civilization-wilderness boundaries, transects perpendicular to the boundaries were established at the nearest clear, simple boundary to the first 50 plots in each area. Here again, three spatial scales were used: 1500 m, 750 m, and 150 m. Transects of these lengths sample the equivalent of six

ruggedness plots at each of the three scales, measuring three in civilization before crossing the boundary and measuring three in the wilderness. Each transect's elevation was sampled at 31 points (the boundary and 15 points in each landscape category). For the urban comparisons, only the 750 m scale was used and transect centers were required to be at least 100 m apart.

Elevational data were taken relative to the mid-point of the transect (the boundary between wilderness and cultural landscapes). Boundaries created by cultures whose archetypal wilderness is based on topography rather than plant community likely run more perpendicular to the slope of the land, thus the transects should show maximized elevational gradients. In contrast, the boundaries created by cultures with land cover based wilderness archetypes are likely to be less perpendicular to the topographic slope, meaning that the elevational gradient measured along a transect perpendicular to the boundary may be somewhat lower than the true slope. Additionally, plant community-based wilderness archetypes should lead to greater variation in relative elevation among transects with transect segments on either side of the civilization-wilderness border both above and below the border elevation. The presence of positive and negative relative elevations should further depress the elevational means in these cultures. The absolute values of the coefficients of variation ( $|CV|$ ) were used to combine the variability and means of the sampling positions along the transects. Using the absolute values of the CV's allowed direct comparison of deviations from the boundary elevation regardless of whether they were above or below. Thus the  $|CV|$ 's of topographically defined border transects were expected to be lower (lower standard deviation and higher mean) than the  $|CV|$  of vegetation defined transects. To detect

differences between the |CV|'s along the relative elevational transects of Germany and Korea, 95% CI's were established for the |CV|'s of the German and Korean wilderness boundary transects using bootstrapping with 1,000 replicates and the percentile method (Efron 1981).

The relative elevational transect |CV| profiles of Korean and non-Korean cities were compared using repeated measures MANOVA after the data were log-transformed to meet the assumption of normality. The 95% CI's of the two means were established using bootstrapping with 1,000 replicates and the percentile method (Efron 1981).

## **Results**

### **Wilderness Archetypes**

German and Korean folk tales each showed a clear wilderness archetype. German folk tales had 92 mentions of forest, which exceeded the Peirce's criterion limit (PCL) of 59.9. Korean folk tales had 54 mentions of mountains, which exceeded the PCL of 40.0. Both German and Korean protected area names exhibited the same wilderness archetype as their folk tales (German<sub>forest</sub> = 31, PCL = 29.6; Korean<sub>mountains</sub> = 48, PCL = 27.2; Figure 6-2A,C). No wilderness type exceeded the PCL for either Irish folk tales or Irish protected area names (Figure 6-2B). However, wilderness types mentioned in Irish folk tales and protected area names were significantly correlated ( $n = 12, r = 0.71, p = 0.01$ ).

### **Land Use Patterns**

#### **Ruggedness index**

All the logistic regressions for transitions between civilization and wilderness were significant (Table 6-2). As expected, the logistic regressions for Korea (at all scales and including the urban sampling) tended to have greater  $-\log$  likelihood

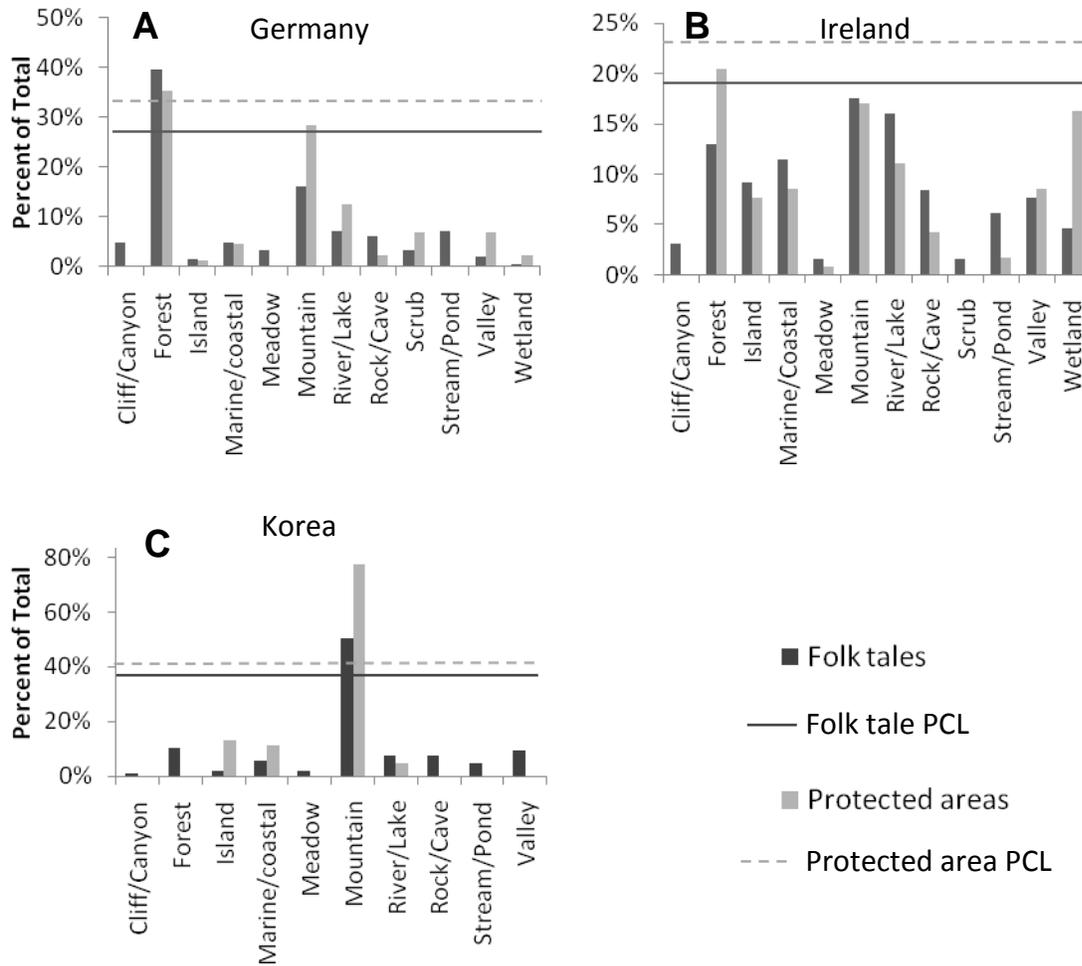


Figure 6-2. Comparisons between the wilderness archetypes reflected in folk tales and the geographical references in protected area names for A) Germany, B) Ireland, and C) Korea. Peirce's criterion limits (PCL) are indicated. Geographical categories exceeding their limit are outliers and considered indicative of cultural wilderness archetypes. Note that the "Mountain" categories are exaggerated in Germany and Ireland by using the Korean perception, lumping hilly terrain with truly mountainous terrain.

differences from the null, higher  $r^2$  values, and greater areas under ROC curves than the non- Korean data sets (Table 6-2) indicating that the transition from civilization to wilderness is more predictable based on ruggedness in Korea than in German mountains (Figure 6-3) and in Korean urban areas than in non-Korean urban areas

(Figure 6-4). The exceptions to this general pattern were Los Angeles and Seoul-Incheon and Busan, which overlapped in some metrics.

Table 6-2. Logistic regression results for the ruggedness index (RI) plots for Korea and Germany (at three scales) and the Korean and non-Korean large urban areas.

	Neg. Log-likelihood <sup>a</sup>	r <sup>2b</sup>	Area under ROC curve <sup>c</sup>	Inverse prediction (m) <sup>d</sup> (95% CI <sup>e</sup> )		
				95%	50%	5%
Korea 250 m	69.3	1.00	1.00	78	80	82
Germany M 250 m	32.3	0.47	0.90	(-72) 7 (45)	(110) 135 (168)	(216) 263 (367)
Korea 125 m	69.3	1.00	1.00	42	43	44
Germany M 125 m	29.4	0.42	0.89	(-44) 1 (23)	(60) 74 (91)	(122) 147 (201)
Korea 25 m	44.7	0.64	0.97	(-3) 4 (7)	(12) 14 (18)	(21) 25 (34)
Germany M 25 m	21.5	0.31	0.85	(-14) -2 (4)	(13) 16 (20)	(28) 35 (48)
Seoul-Incheon	48.3	0.70	0.97	(-7) 16 (28)	(41) 50 (64)	(69) 84 (121)
Busan	50.2	0.72	0.98	(-3) 36 (54)	(71) 86 (102)	(116) 136 (178)
Daegu	69.3	1.00	1.00	42	43	43
Gwangju	69.3	1.00	1.00	40	41	41
Daejeon	58.0	0.84	0.99	(-1) 26 (36)	(41) 50 (66)	(60) 74 (119)
Sao Paulo	13.3	0.19	0.76	(-119) -36 (-6)	(37) 51 (68)	(105) 137 (229)
Mexico City	26.7	0.39	0.91	(-77) -27 (-2)	(41) 56 (75)	(109) 138 (201)
Los Angeles	50.4	0.73	0.97	(-27) 13 (33)	(55) 72 (97)	(104) 132 (195)
Istanbul	11.8	0.17	0.78	(-131) -40 (-8)	(38) 53 (71)	(112) 147 (246)
Rio de Janeiro	22.3	0.32	0.80	(-131) -52 (-19)	(36) 55 (80)	(121) 161 (264)

<sup>a</sup> The difference between the -log likelihood of the logistic models and the null model (no relationship)

<sup>b</sup> p < 0.0001 for all regressions

<sup>c</sup> The area under the ROC (Receiver Operating Characteristic) curve indicates the ability of the model to correctly categorize a RI as civilized or wilderness. Perfect predictive ability = 1.00, no predictive ability = 0.50

<sup>d</sup> The inverse prediction gives the RI that results in a 95%, 50%, and 5% probability of being civilized.

<sup>e</sup> Confidence Interval

The inverse predictions from the logistic regressions followed expectations in the two larger scales (250 and 125 m plots) with the Korean 95%, 50%, and 5% civilization

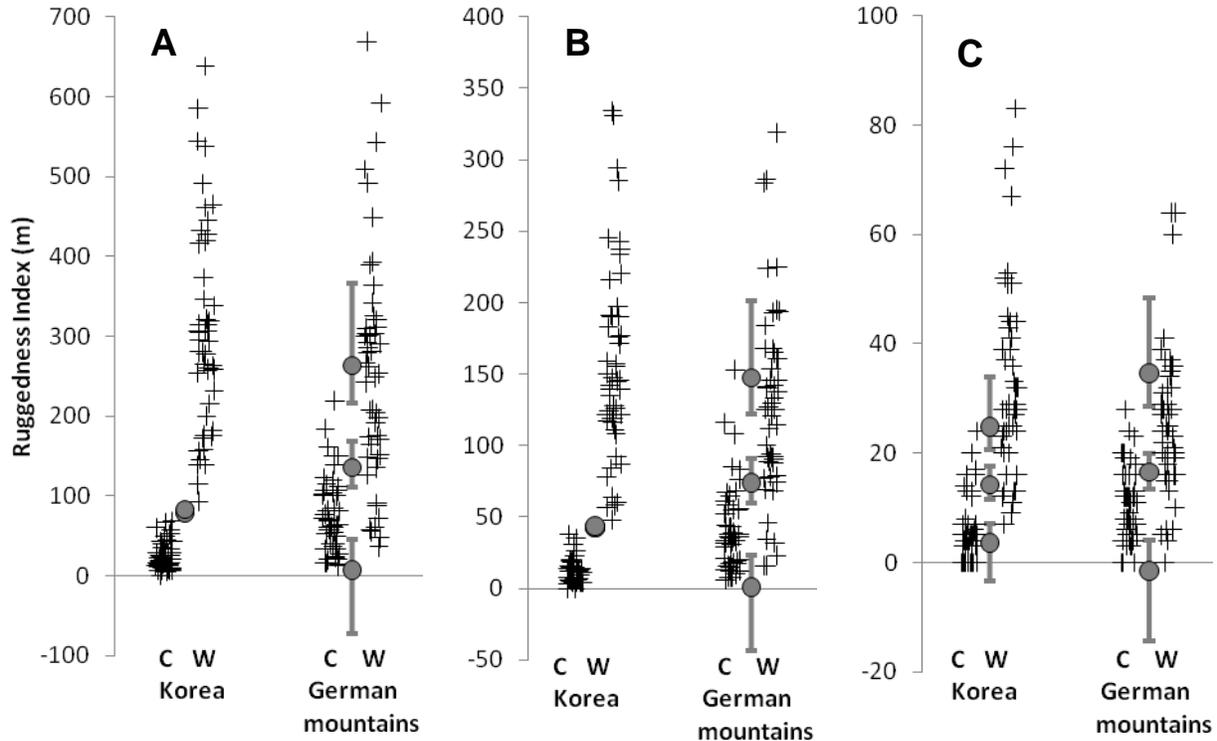


Figure 6-3. Ruggedness indices of civilized and wilderness plots in Korea and German mountain areas at three scales (n = 50 for each category): A) 250 m plots, B) 125 m plots. C) 25 m plots. Note the lack of overlap between the Korean plots but wide overlap between the German plots in A and B. At the smallest scale (C), the pattern begins to break down. The data have been jittered on the horizontal axis to show overlapping points. Gray circles represent the 5%, 50%, and 95% logistic regression inverse predictions with 95% confidence intervals. C = Civilized plots; W = Wilderness plots

probabilities occurring within a very narrow range (essentially at the same point) and those of the German mountains widely spread with non-overlapping CI's. This indicates a very distinct transition from civilization to wilderness based on ruggedness in Korea that is lacking in Germany. Also, the Korean 50% probabilities were lower than the CI's of the German mountain 50% probabilities (Figure 6-3A and B), indicating a higher tolerance for ruggedness in civilized areas in Germany. However, at the smallest scale (25 m),

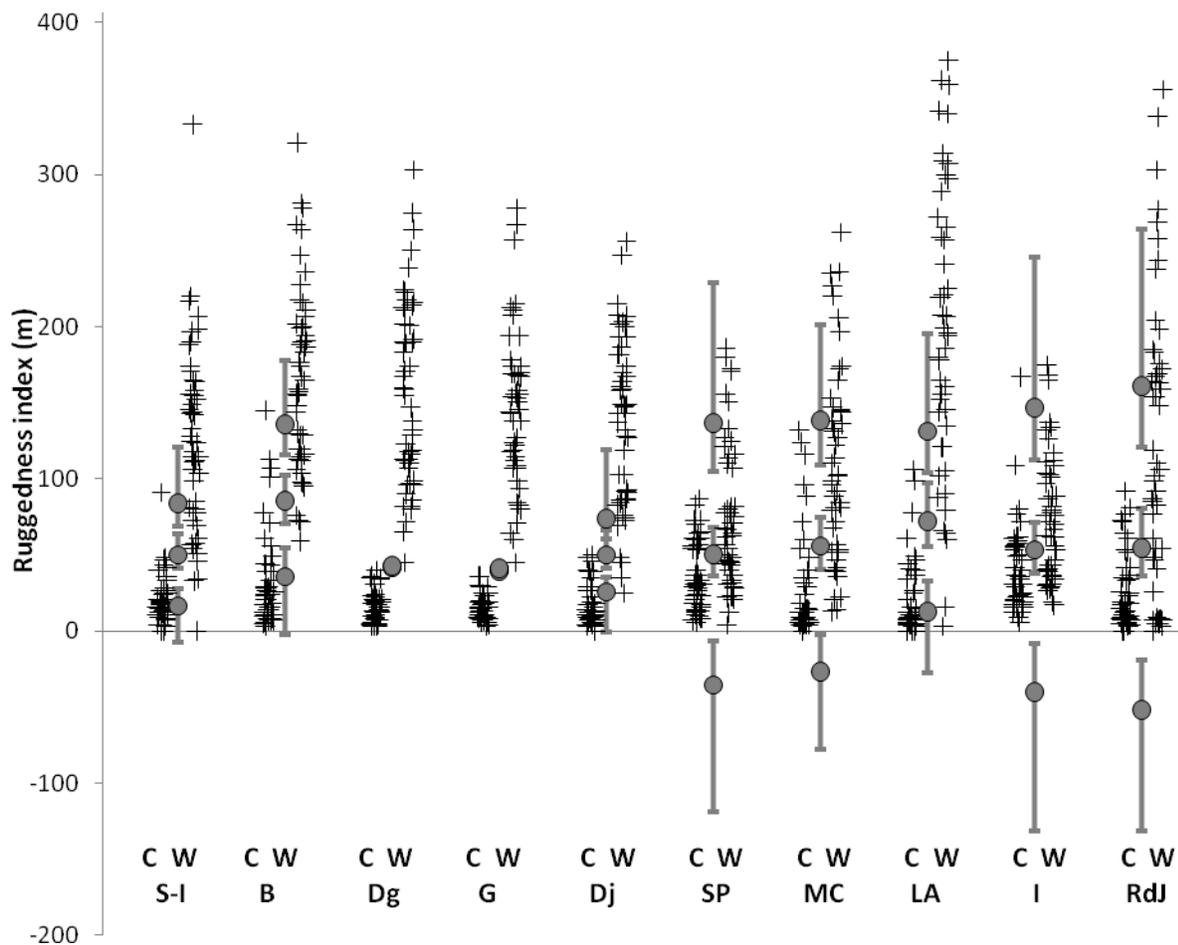


Figure 6-4. Ruggedness indices of civilized and wilderness plots in Korean and non-Korean large urban areas (125 m plots,  $n = 50$  for each category). The data have been jittered on the horizontal axis to show overlapping points. Gray circles represent the 5%, 50%, and 95% logistic regression inverse predictions with 95% confidence intervals. C = Civilized plots; W = Wilderness plots; S-I = Seoul-Incheon; B = Busan; Dg = Daegu; G = Gwangju; Dj = Daejeon; SP = Sao Paulo; MC = Mexico City; LA = Los Angeles; I = Istanbul; RdJ = Rio de Janeiro

the pattern disappears and the CI's of the three civilization probabilities of Korea overlap their counterparts in the German mountains (Figure 6-3C).

The ranges from the 95% to the 5% civilization probabilities were significantly smaller in Korean urban areas than in non-Korean urban areas ( $\bar{x}_K = 43.6$ ,  $\bar{x}_{n-K} = 171.2$ ,  $t = 5.16$ ,  $p < 0.001$ ) indicating that Korean urban areas have a sharper transition (Figure 6-4). Surprisingly, however, the 50% civilization probabilities were not different ( $\bar{x}_K = 53.8$ ,  $\bar{x}_{n-K} = 57.3$ ,  $t = 0.39$ ,  $p = 0.355$ ).

### **Border transects**

Borders between wild and civilized areas were generally quite sharp and obvious. At all three scales (1500, 750, and 150 m), the Korean relative elevational border transects showed S-shaped profiles (Figure 6-5 A-C) while the German mountain border transects were more symmetrical with unkempt “bowtie” profiles (Figure 6-5 D-F). The |CV|’s of the German transects were generally higher than those of Korea. However, not all sampling locations had non-overlapping CI’s (1500 m scale: 8/30 non-overlapping sampling locations; 750 m scale: 30/30; 150 m scale: 29/30; Figure 6-6).

The Korean urban area border transects also showed S-shaped profiles (Figure 6-7 A-E) while the non-Korean urban area border transects were more symmetrical with unkempt bowtie profiles similar to those in Germany (Figure 6-7 F-J). The profile of the Rio de Janeiro transects is the most similar to that of the Korean transects; however, Rio de Janeiro differs from the Korean urban areas in having a concentration of flat transects, especially on the wilderness side (Figure 6-7 J). The means of the Korean urban border transect |CV|’s were significantly lower than those of the non-Korean urban areas ( $F = 15.1$ ,  $p = 0.005$ ). All of the Korean urban relative elevational border transect |CV|’s were lower than the lowest of the non-Korean urban areas and the 95% CI’s of the means did not overlap (Figure 6-8).

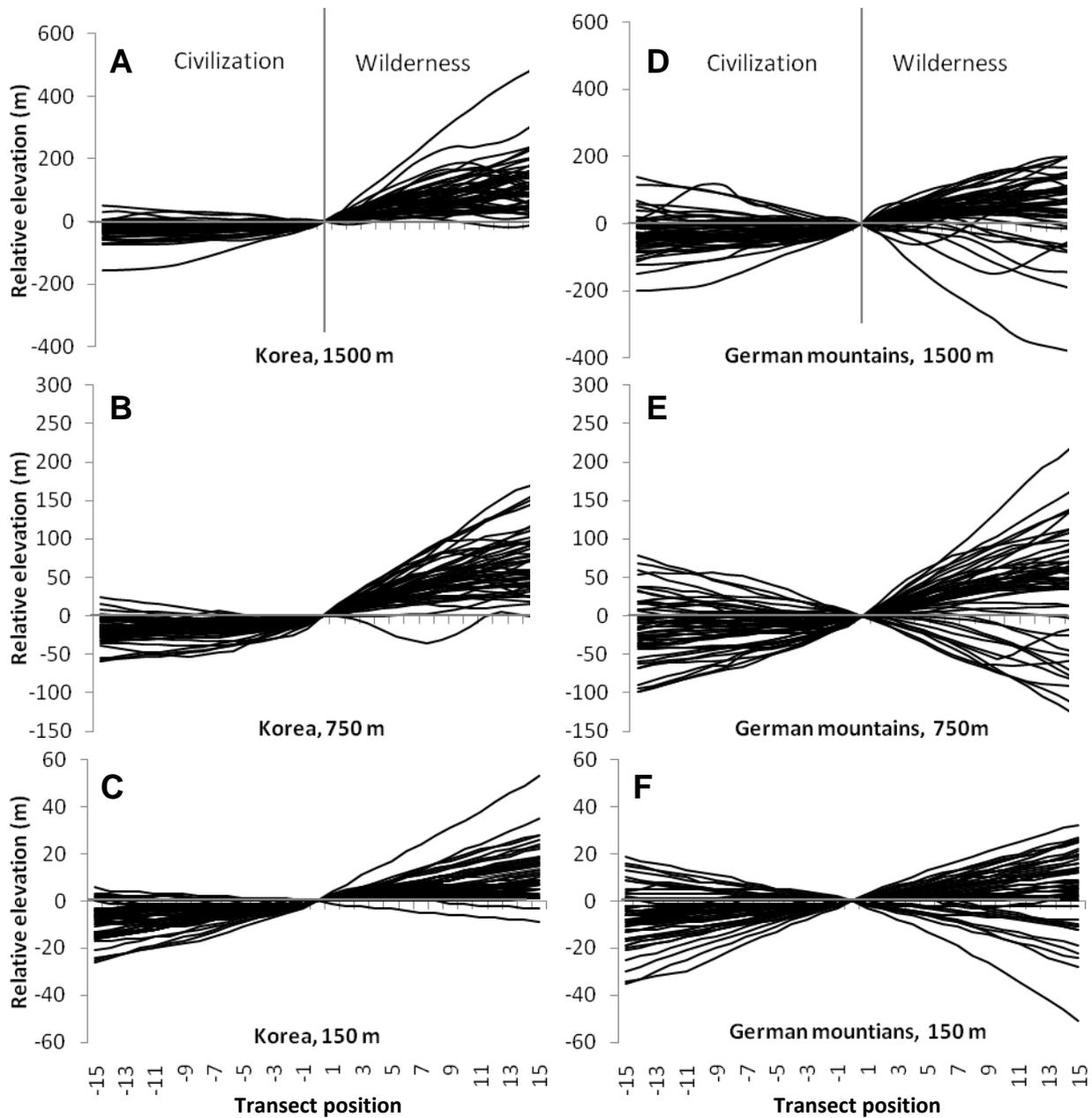


Figure 6-5. Relative elevational transects perpendicular to and centered on the civilization-wilderness boundaries in Korea and German mountain areas at three different scales ( $n = 50$  for each set): 1500m, 750 m, and 150 m. Note that Korean transects exhibit an S-shaped profile while transects in the German mountains have a more symmetrical unkempt bowtie-like profile.

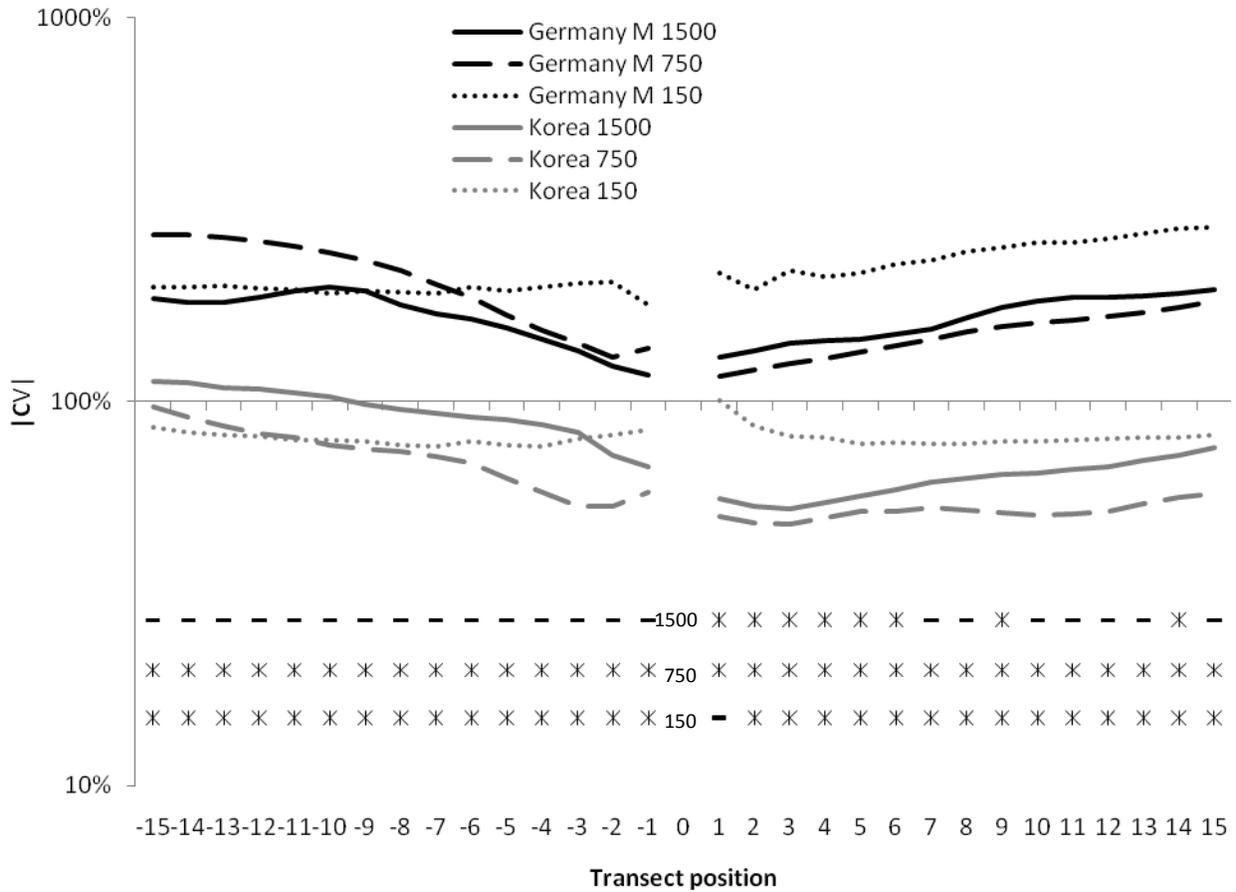


Figure 6-6. Coefficients of Variation for the civilization-wilderness boundaries in Korea and German mountains for three different transect lengths (1500 m, 750 m, and 150 m;  $n = 50$  for each set). Symbols at the bottom of the graph indicate overlapping (-) and non-overlapping (\*) confidence intervals at each sampling location for each scale.

## Discussion

### Wilderness Archetypes

Both German and Korean folktales showed clear wilderness archetypes (forest and mountain respectively), but Irish folktales did not (see below). The forest is so recognized as the German archetype of wilderness that German culture has often been considered a product of the forests (Chaney 2004, 2005; Imort 2005; Mauch 2004; Radkau 2005; Williams 2005). In Germany, mountainous areas are limited while forests

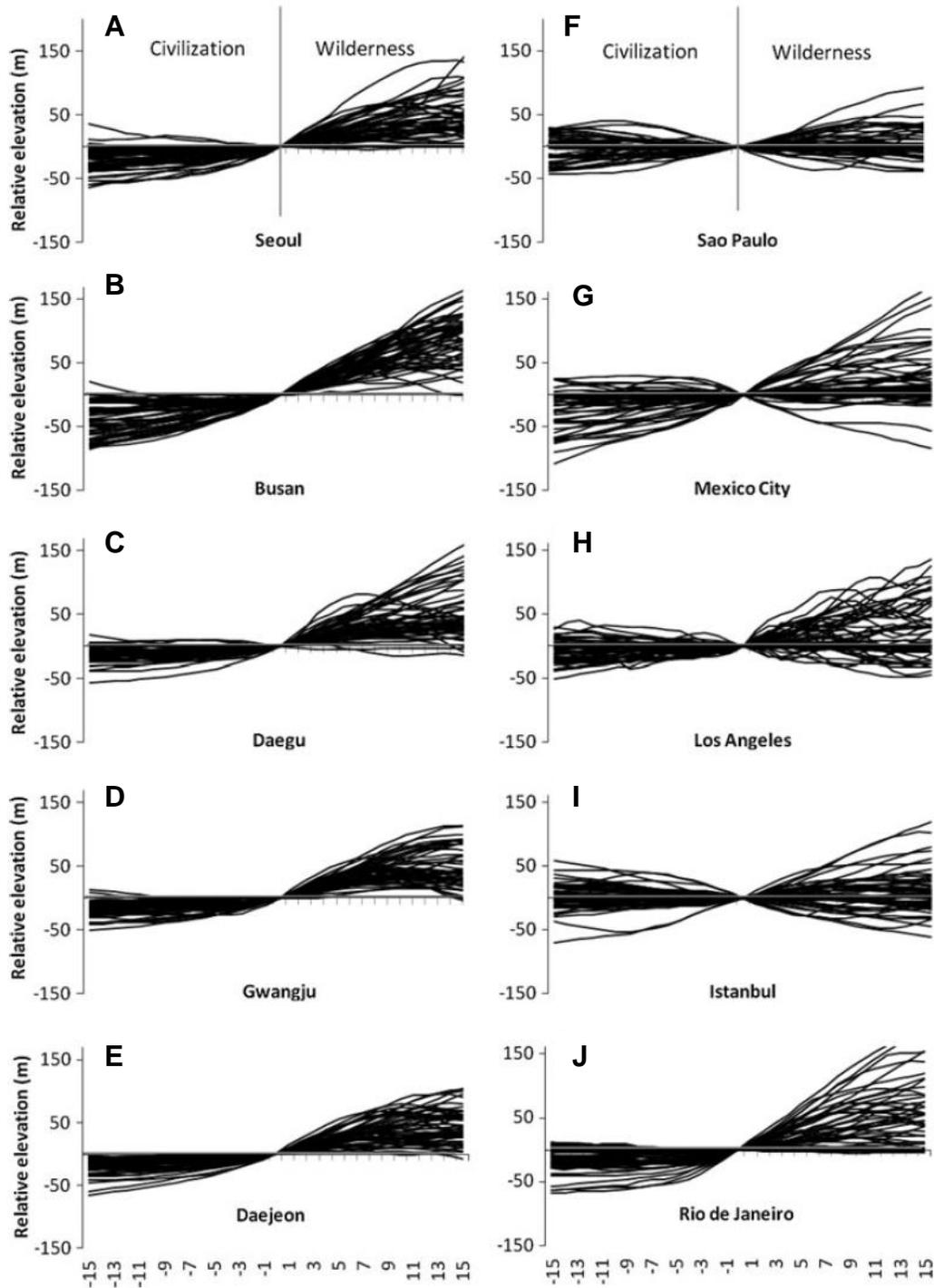


Figure 6-7. Elevational transects perpendicular to and centered on the civilization-wilderness boundaries in Korean and non-Korean large urban areas (750 m,  $n = 50$  for each set). Note that transects from Korean urban areas exhibit an S-shaped profile while those from non-Korean urban areas tend to have more symmetrical unkempt bowtie-shaped profiles.

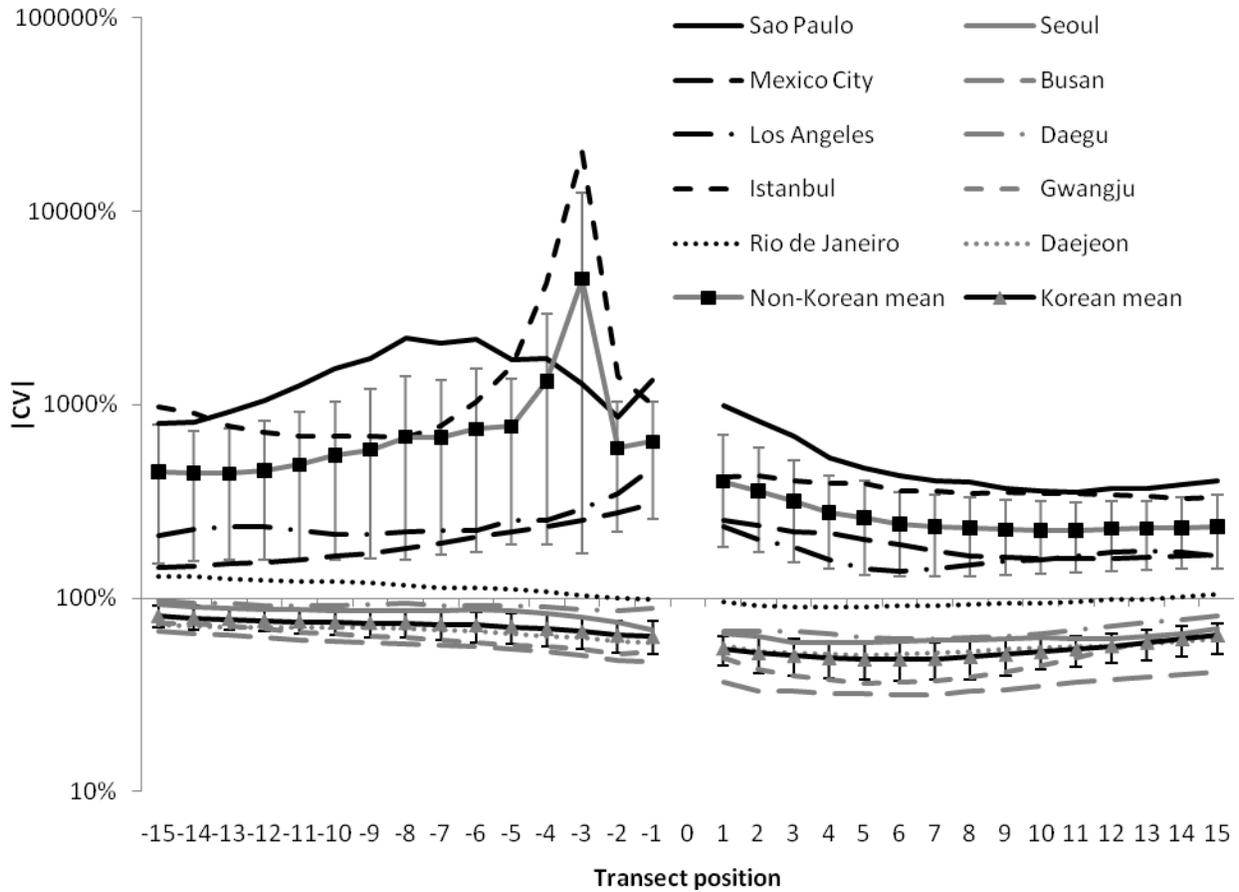


Figure 6-8. Coefficients of Variation for the relative elevational transects centered on the civilization-wilderness boundaries in Korean and non-Korean large urban areas (n = 50 for each set). The means and 95% confidence intervals of the two groups are also indicated.

were widespread. Thus mountains would have been less important to the average German than the thick, often swampy forests which are considerable obstacles for farming, grazing livestock, and travel. These conditions help explain the growth of a landcover-based wilderness archetype in Germany. On the other hand, Korea, while originally heavily forested (South Korea is still ~66% forested; (Park et al. 2000), is also a largely mountainous peninsula, thus providing opportunities for both mountains and forest to serve as the pan-Korean wilderness archetype.

There are several probable reasons for the clear dominance of mountains as the Korean wilderness archetype. Mountains and forests both present obstacles to development. However, while forests can be cleared, mountains are more resistant. Even labor-intensive terracing of mountainsides does not eliminate the logistical difficulties caused by the overall slope. In addition to the practical characteristics of rugged terrain, mountains present very different psychological impacts than forests. Mountains visually dominate the surrounding landscape and confer commanding and awe inspiring views in ways forests cannot. The vistas provided by mountains are likely a primary cause of the use of the word “sublime” to describe wilderness (Oelschlaeger 1991). It seems likely that these qualities and the relative closeness of the summits to the sky (often associated with or home to important gods) contributes to the association of mountains with the supernatural in many cultures (*e.g.*, Burnett & wa Kang'ethe 1994), including Korea's.

In addition to the general physical and psychological impacts of mountains, the agricultural economy of Korea has probably played an important part in the development of the mountain wilderness archetype. Rice has been grown in Korea since 2000 – 1500 B.C.E. (Choe & Bale 2002) and has had a far greater cultural importance than would be predicted by the area of land actually under rice cultivation (Lee 1994). This bias has likely been caused by a general preference for rice over other dietary staples, the greater profitability of rice as a crop, and the greater productivity and dependability of paddies over dry fields (Lee 1994). Because of the need to flood rice paddies, topography presents a larger obstacle to rice agriculture than forests as carving rice paddies out of a mountainside necessitates not only the clearing

of the forest but the major engineering feat of terracing. Even though other staple and minor crops can be grown in upland fields, the cultural dominance of rice probably influenced the rise of mountains as the Korean wilderness archetype.

The development of a mountain wilderness archetype was plainly not influenced by any technological or logistical inability to build in the mountains as evidenced by the preferential construction of temples (historically and currently) and large fortresses (historically) in the mountains. These developments are isolated from the rest of the cultural sphere by wilderness, which can be desirable for defensive or spiritual reasons and are clear exceptions to normal land use patterns. Small farms and settlements can also be found in the mountains. However, the discovery of derelict fields and homes only in the mountains and not in the lowlands (through the sampling during this study and pers. obs.) indicates that such locations are likely considered marginal and not rapidly reclaimed once abandoned.

Unlike Germany and Korea, Ireland did not show any clear wilderness archetypes. Based on the historic importance of cattle and dry field agriculture in Ireland, as well as the original heavily forested landscape with large wetland areas (Raftery 1994), it was expected that an Irish wilderness archetype would be forest, wetland, or both. Because Irish wetlands are common and associated with obstacles to travel, ancient religious significance, and extraordinary finds (Irish elk antlers, Gould 1974; ancient artifacts, Raftery 1994), they were expected to have particular significance. However, wetlands were ranked 9<sup>th</sup> out of 12 wilderness types in folktales. Another unexpected observation in the Irish tales was the seemingly high number of anthropogenic places around which the magical or dangerous parts of the story centered without reference to a surrounding

natural landscape. Interestingly, most of these locations were ancient raths and Neolithic tumuli, which were likely to have been viewed by the storytellers as having been built by the old gods or fairies, not by humans.

The occurrences of habitat types in the protected area names of the three nations reflected the wildernesses gleaned from their folktales. Even Ireland, which lacked a clearly defined wilderness archetype, had a significant correlation between the habitat types mentioned in folktales and in the protected area names. While these results suggest that traditional wilderness archetypes are persistent and pervasive and are reflected in the names of protected areas, other factors likely influence the naming of protected areas.

First of all, it could be posited that a correlation should exist between mentions of habitat in folktales and in protected area names under null conditions: there is no development of a wilderness archetype and habitat types appear in both the folktales and in protected area names simply in the proportion in which they exist within a nation's borders. This may be the case with the Irish data presented here. However, given that traditional wilderness archetypes probably develop over much longer time scales than protected areas are gazetted and renamed, it is unlikely that null derived distributions would be well matched as they should reflect different time periods with different habitat proportions. Additionally, in the case of Germany, presence of a forest wilderness archetype is consciously recognized, while in Korea the null model would predict forests and mountains to be almost equally represented as mountains are generally forested, which is clearly not the case.

Secondly, conservation status may impact naming decisions. For example, especially rare or endangered habitat types are likely to be disproportionately targeted for conservation and disproportionately mentioned in protected area names. This bias probably explains the high occurrence of wetlands in Irish protected area names as well as similar high occurrences of wetlands in the protected areas of some other nations (e.g., France and Serbia; Worman unpub. data).

Thirdly, areas may be purposefully excluded from protected area status predicated on the assumption that their inaccessibility is protection enough (and also hampers tourism). In this case, wilderness archetypes would be underrepresented due to the sharpened perception of their inaccessibility. For example, the Rwenzori Mountains of Uganda were passed over for national park status in the 1950's by the British (Willock 1964) due to their inaccessibility. In spite of this, they, and other mountainous areas in Uganda, have subsequently been gazetted as national parks and are threatened by encroachment.

Fourthly, the term "protected area" encompasses many different types with different goals, both of which vary from country to country. For example, in the United States, Wilderness Areas and Wildlife Refuges have very different dominant habitats (mountains and rivers/lakes, respectively; Worman unpub. data) related to their different goals. Thus, different types of protected areas can bias the data if they have divergent goals.

With these caveats in mind, the suggestion that protected area names reflect cultural wilderness archetypes is supported by the examination of some specific examples. In Korea, Naksan Provincial Park is a typical beach/coastal park with the

border running parallel to and enclosing the shoreline but not running far inland. This park, though, is named after a small nearby hill (*Naksan* = “Joy Mountain”) with a temple. Another Korean example is Mun-gyeongsaejae Provincial Park, a valley park surrounded by a high ridge. Though the ridgeline is not actually within the borders of the park, the name of the park focuses on the ridge and its height (*saejae* = “bird ridge” reportedly implies that the ridge is an obstacle even to birds; Jeong S.-Y., pers. com.). Such is the strength of the Korean wilderness archetype and its spiritual and recreational significance (as evidenced by the placement of temples and tombs in the mountains and the throngs of weekend mountaineers; pers. obs.) that protected areas are sometimes branded with montane monikers even when they protect entirely different landscapes. Similar cultural importance is evident in the frequent use of the German wilderness archetype in attempts to unify a frequently divided people with a common binding forest mythology (Chaney 2004; Imort 2005).

## **Land Use Patterns**

### **Ruggedness index**

The importance of topography on human settlement patterns in general is clearly shown by the significance of all the RI logistic regressions. It is interesting, however, that finer differences are evident between cultures. At the largest two scales, the RI shows that Korea has very clear and sharp transitions between civilization and wilderness, while Germany has ranges of RI shared by both civilization and wilderness. There are also indications that the 50% transition point in Germany is higher than in Korea. It appears that Korea is less likely to develop mountains than is Germany. Both of these results were expected as a deforested mountain is still a mountain but no longer a forest and thus still fits into the Korean, but not the German, archetype of

wilderness. If wilderness is perceived to be inappropriate for settlement by people in general, it would explain the apparent Korean reluctance to develop rugged areas.

The loss of differences between the Korean and German profiles at the smallest scale (25 m) appears to be due to plots that contained both civilization and wilderness (mixed plots) at the two larger scales shifting into the civilization category as the plot size was reduced. This is evidenced by the fact that these plots in Korea, ranging from RI 0 m to 24 m, were the only civilized plots at that scale above RI 8 m (Figure 6-3). In comparison, the same type of plot in Germany ranged from RI 7 m to 24 m with plots that had been civilized at both larger scales ranging from RI 0 m to 24 m and with plots that had been mixed at the largest scale but civilized at the medium scale ranging from RI 3 m to 28 m. That, in Korea, these more rugged plots only appear in the civilized column at the smallest scale indicates that development in rugged areas is smaller and patchier than in Germany.

The comparisons between Korean urban areas and large non-East Asian urban areas show patterns similar to the Korean-German comparisons. Again, Korea shows much sharper transitions between the ruggedness of civilization and wilderness with smaller ranges of overlap than non-Korean urban areas (Figure 6-4). The Korean urban areas (like Korea in general) showed an almost total lack of any relatively flat wilderness plots (a single coastal wetland plot near Seoul-Incheon was the only exception and the only wetland sampled in Korea). The scarcity of wetland wildernesses is probably due to a combination of natural Korean topography and the value of wetlands as areas for rice farming, as well as the intensive use of low-lying areas due to the reluctance to develop mountains.

The typical Korean ruggedness profile at the medium scale (both for Korea in general and the urban areas) shows an RI cutoff of around 40 m, below which there are almost entirely civilized plots and above which there are almost entirely wilderness plots (Figure 6-3B and 6-4). Busan appears to be the most divergent with civilized plots continuing up to an RI of 145 m and the wilderness plots beginning at an RI of 59 m. Busan's divergence from the typical Korean profile is probably due to its being a major port city in a fairly rugged area, tied spatially and economically to its harbor but without much flatland to develop. Thus, as Busan grows, the extreme scarcity of flatland likely causes development to gradually push up the sides of the mountains. The generality of this pattern is supported by the observation that the outlier from the civilized plots in Seoul-Incheon (at RI 91 m) is a new apartment complex built on the side of a mountain, apparently on previously undeveloped land and not an older established neighborhood or farmland judging from the surrounding and encompassed vegetation.

For the non-Korean urban areas, the RI profile of Los Angeles appears to be most similar to those of the Korean urban areas (Table 6-2, Figure 6-4). This similarity is most likely not due to any unwillingness on the part of Los Angelinos to develop rugged areas. On the contrary, hill- and mountainside homes are in high demand, in spite of the dangers of earthquakes, fires, and debris flows in the area (McPhee 1989). Rather, the similarity between the Los Angeles ruggedness profile and those of the Korean urban areas seems to be an artifact of sampling. The rugged areas in Los Angeles are extremely limited compared to the extent of the total urban area, which is largely flat. Thus, while development in rugged areas may be preferred (though costly) for some

uses, few of the plots fell in civilized mountainous areas because of the limited proportion of mountainous terrain within Los Angeles itself.

Interestingly, though the ranges encompassed by the 95% and 5% civilization probabilities are larger in the non-Korean urban areas, the 50% civilization probabilities are not different. These results indicate that there may be similar decision rules across cultures with regards to ruggedness and development. However, Korea, with its mountain wilderness archetype, appears to follow the rule more strictly than other cultures.

### **Border transects**

The relative elevational civilization-wilderness border transects for Korea at all three scales and for Korean urban areas showed consistent S-shaped profiles with the civilized half of the transects flat and slightly below the elevation of the border and the wilderness half curving above the border elevation (Figures 6-5 and 6-7). The German and non-Korean urban areas, on the other hand, showed more symmetrical profiles on both axes, giving the impression of more or less unkempt bowties. However, here too the civilization side tends to appear flatter and the wilderness side more positive, indicating, like the ruggedness indices, the universal impact of topography on settlement patterns.

The |CV|'s of the elevational transects are consistently (and largely significantly) lower in Korea and Korean urban areas than in German mountains and non-Korean urban areas, respectively (Figures 6-6 and 6-8). It is notable that this metric apparently discriminates better than the RI, with Los Angeles, Busan, and Seoul well contained within their respective groups. Additionally, Busan, which had high ruggedness limits for its civilized plots, has the most "Korean" of the |CV| profiles. Looking at the

elevational transect profile (Figure 6-7B), it can be seen that the civilized half of the transects often dip farther below the civilization-wilderness border than typical for Korean cities, suggesting again that development in Busan has pushed up the mountainsides, probably due to severe crowding of the flatlands.

There is much more variation among the |CV| profiles of the non-Korean urban areas (Figure 6-8). This is not surprising as they are drawn from different geographic and cultural areas around the world. It is interesting to note that the Rio de Janeiro |CV| profile dips closer to the Korean urban areas than its own grouping, although distinctly different from the Korean urban areas based on the ruggedness indices (Table 6-2, Figure 6-4). This similarity is due to the lack of developed hills in the Rio de Janeiro transects. However, the differences between Rio de Janeiro and the Korean urban areas (the slightly higher |CV| profile and ruggedness indices) are due to the flat wetland wildernesses in Rio de Janeiro (Figure 6-7J).

### **Conclusions and Conservation Implications**

The differences between the Korean and German land use patterns are consistent with the hypothesis that they are influenced by wilderness archetypes. The null expectation that apparent differences in land use patterns are caused by nations with higher population densities being forced to develop topographically undesirable areas predicts the opposite of what was observed here. Korea has a higher population density (South: 478 people/km<sup>2</sup>, North: 195 people/km<sup>2</sup>, total: 322 people/km<sup>2</sup>) than does Germany (231 people/km<sup>2</sup>) (UN 2008), yet its land use is guided more by topography, not less, indicating the potential importance of cultural details like wilderness archetypes.

This study raises several questions about the nature of wilderness archetypes: how common, specific, strong, persistent, and intraculturally variable are wilderness archetypes? There are likely other types beyond the two broad categories examined here (topographic and land cover), such as aquatic or even seasonally or daily variable. It may appear that topographic wilderness archetypes would be more common than land cover archetypes because of the difficulties presented by rugged terrain; however, judging by the comparisons of the urban areas, topographic wilderness archetypes may actually be rarer than land cover archetypes. It seems likely that certain characteristics would increase the chances of the development of topographic wilderness archetypes in a culture: fairly rugged native terrain, an economic system strongly affected by terrain (such as rice farming), and ties with another culture having a topographic archetype. This is not to say that mountains are necessarily the only topographical wilderness archetype possible. In certain situations, the mountains themselves may be a culture's home terrain, perhaps providing safety from marauding enemies or flooding rivers or by providing better environmental conditions (e.g., better for crops or livestock or fewer problems with disease). In these cases, a wilderness archetype might develop in which the valleys or lowlands were the archetypical wilderness.

When a wilderness archetype is present in a culture, the attitudes towards the wilderness and those in it (both negative and positive) are likely to have the effect of keeping the wilderness undeveloped and outside the cultural sphere. Negative attitudes (e.g., fear, revulsion, and suspicion) will tend to decrease the probability of development in an archetypical wilderness, while positive attitudes (e.g., appreciation of beauty, recreation, ecosystem functions, and material value) will tend to increase the probability

of protection of an archetypical wilderness. A clear example of the latter occurred when the German empire gazetted forest reserves in Tanganyika. The areas protected and managed as forests were almost completely closed canopy montane forests but the much more widespread open miombo woodlands were not recognized as true forests and were thus excluded from forestry reserves (Sunseri 2005).

While a wilderness archetype may somewhat protect a certain habitat or landscape type, it is likely at the expense of others as development is then concentrated in non-archetypical wilderness areas. Decreased development of archetypical wildernesses is probably most extreme in the cases of topographically defined wildernesses as it is much easier to alter land cover than elevation. For example, in Korea the land use pattern that has left the mountains largely untouched has concentrated development in valleys and along rivers, and continues more recently in the so-called reclamation of marine mudflats.

In addition to the increased representation in the non-anthropogenic landscape of the archetypical wilderness, the reluctance to develop an archetypical wilderness likely results in less fragmentation. Again, this is probably more pronounced with topographically defined wildernesses. An archetypical wilderness is likely to be devoured from the edges more so than other habitat types as people may generally be reluctant to settle deeply within it. However, the rate of development on any boundary is likely to be uneven (especially for land cover defined wildernesses), altering the degree of fragmentation. Korea and German mountains exhibit these patterns clearly: in Korea, forest is rarely found isolated in patches as it follows the ridges of the mountains, but in Germany, forest patches occur more frequently as forest clearing

does not follow the terrain as closely (Figure 6-9). Furthermore, wilderness archetypes are likely to be more spatially and temporally stable habitats as human use shifts through the landscape preferentially disturbing other habitat types. Because land cover wildernesses can be cleared but recover, the interplay between recovery and consumption may create shifting spatial patterns of wilderness/civilization interaction that cannot occur with topographical wildernesses. More stable and thus older archetypical wilderness communities could in turn strengthen the cultural archetype.

Another layer of complexity is added by considering the cultural attitude towards wilderness. Cultures with positive attitudes towards wilderness should be more likely to allow or actively preserve patches of their archetypical wilderness in close proximity to settlements while cultures with negative attitudes towards wilderness should be less likely to tolerate patches of their wilderness archetype near settlements. Thus, on a larger scale, the existence of a wilderness archetype likely discourages development embedded in the wilderness, but on a smaller scale the attitudes towards the wilderness likely influence tolerance of archetype patches embedded in cultural landscapes.

Incorporating local cultures can be an effective way of engaging communities in conservation programs through the celebration of positive cultural attitudes towards wildlife (Kuriyan 2002) and the use of traditional methods of conflict resolution (Lepp & Holland 2006). Wilderness archetypes provide another motivation to tailor conservation strategies to the local culture. It may be easier to introduce the concept and practice of protected area conservation if an archetypical wilderness is used as a flagship. Also, conservation is most likely to be successful when more traditional valuations of wilderness (e.g., extractive, aesthetic, national, and spiritual) are allowed to prosper

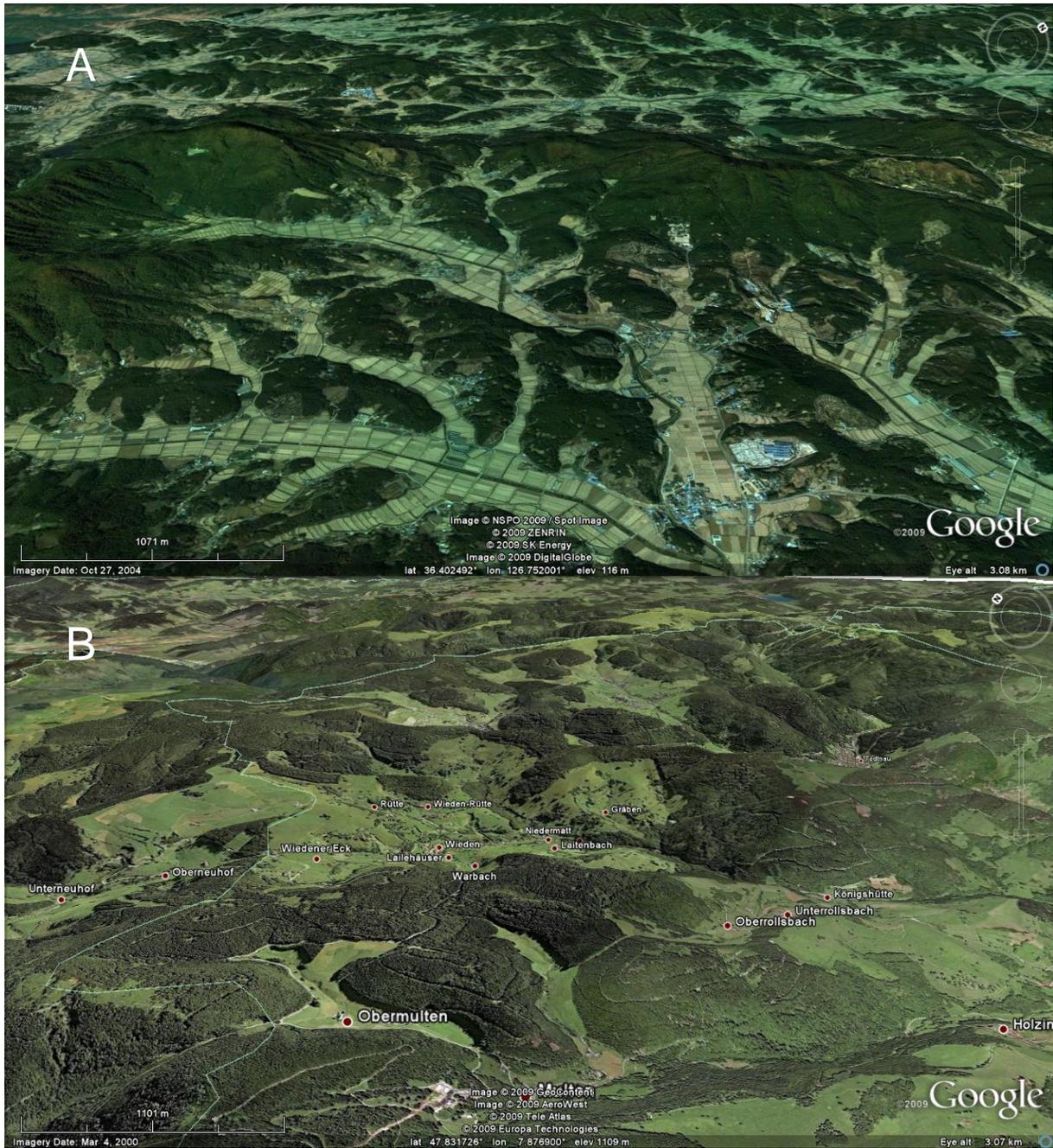


Figure 6-9: Google Earth images of characteristically A) Korean and B) German mountain development patterns. Note how the Korean development is focused in the lowlands leaving the uplands largely forested (the exceptions being generally due to forest management for timber extraction and not development per se), whereas the German development is less bounded by topography. (Korean: Image © NSPO 2009/Spot Image, © 2009 ZENRIN, © 2009 SK Energy, Image © 2009 DigitalGlobe; German: Image © 2009 GeoContent, Image © 2009 Aero West, © 2009 Tele Atlas, © 2009 Europa Technologies.)

alongside more recent valuations (e.g., tourism, ecosystem services, and biodiversity), thus maintaining and strengthening the idea and worth of wilderness in the local culture. However, as suggested by this study, non-archetypical wilderness areas may be in greater, more immediate need for protection as they are likely to be more threatened by development. Thus while wilderness archetypes may be useful for introducing conservation, subsequent education about the benefits of conservation should specifically address the different values of different habitats emphasizing those in most danger.

Unfortunately, increasing population pressure and globalization are likely to speed cultural change and eventually break down traditional cultural and psychological barriers to development in archetypical wildernesses. These shifts could result in increasing development of previously avoided wilderness areas, necessitating a reevaluation of conservation priorities. Thus, wilderness archetypes are important to conservation not only because of their influence on past and current land use patterns and their worth in promoting conservation, but also because of their potential for change.

## CHAPTER 7 CONCLUSION

Understanding anthropogenic impacts on the biosphere is arguably among the most important and urgent tasks for biology today. Synthesizing the impacts of thousands of different cultures with vastly different extractive strategies on countless complex, interconnected, and poorly understood ecological systems is daunting. This study has suggested that one step towards such a synthetic understanding is provided by examining anthropogenic impacts as a broad and unified gradient and applying this general gradient and its effects to considering how a specific and understudied ecosystem process, animal-mediated nutrient transfer, changes along this gradient. This permits one to conceptually examine the potential ramifications of anthropogenic change on one key aspect of nutrient flows. Then through the use of a model organism in a field system, the real-world impact of predicted anthropogenic changes was studied experimentally and observationally under field conditions. Finally, modifications to the general gradient of anthropogenic effects were suggested to arise based on cultural perceptions of wilderness and resulting land use differences. This hypothesis was examined through a combination of approaches taken in anthropology and landscape ecology.

The first part of this study (Chapter 2) suggested that there is a spatio-temporal gradient of anthropogenic influence on biotic systems ranging from low-density hunting, through pastoralism and then the wide range of agricultural practices and densities, to higher-density habitation from suburban to urban settlements. It was suggested that along the gradient of anthropogenic influence there are impacts on animal-mediated nutrient transfer through several main routes: maximum body size and home range

decreases of animal consumers, alterations in community change rate, appearances of novel resources, increases in the relative importance of generalists, and combinations of these produce complex changes in the relative importance of top-down vs. bottom-up control. These changes likely influence animal-mediated nutrient transport processes by altering their importance depending on trophic structure, shortening transport distances, increasing the importance of cross-habitat nutrient transfers, and encouraging flow of nutrients into refuge habitats. The increased eutrophication of small refuge fragments is likely to present another challenge to native species in human-dominated landscapes.

Feral Hogs were used as a model generalist-omnivore species that has benefited tremendously from anthropogenic disturbance. In a multi-habitat system located on the Florida Gulf Coast, experimental manipulations (Chapter 3) revealed that hogs had differing impacts on the herbaceous community in the hammock refuge habitat based on landscape patterns, specifically the juxtaposition of marsh feeding habitat. Hog densities were ~4 times higher in the island hammocks embedded in the marsh than in the mainland hammocks along the edge of the marsh, likely due to greater access to feeding areas in the marsh conferred by the islands. Yet exclusion of hogs resulted in increased species richness and percent cover on the mainland but not the islands. This result is suggested to likely be due to a combination of the extirpation of hog-vulnerable plant species from islands with sustained high hog densities combined with the difficulty of dispersing to the islands from mainland populations. Thus, the heavy consumptive and disturbance pressure by hogs has likely created a disturbance-resistant herbaceous community on the islands by filtering out vulnerable species. Herbaceous biomass, on

the other hand, increased in similar amounts in both areas when hogs were excluded, which indicates that even the disturbance resistant communities are under constant pressure. It is unlikely that the influence of the hogs will be reduced without control of their populations and movement patterns by a top predator, such as the Florida Panther, a controlling presence that is currently absent in the system. This study thus suggests that Feral Hogs in Florida are likely having strong impacts on the structure and species composition of at least some plant communities

The nutrient study (Chapter 4) supported the hypotheses that generalist consumers can move nutrients short distances from feeding habitats and concentrate them in refuge habitats. The only important food—established by fecal analysis and confirmed by stable isotope analysis—is bulrush from well-defined patches in the marsh, which is thus the principal source of nutrients transported by the Feral Hogs. The fact that the coastal hog diet is composed almost entirely of bulrush and the observation that the bulrush areas are the only marsh community the hogs root and the rooted patches of the marsh are the only place where bulrush grows implies a tight ecological mutualism between the Feral Hogs and the American Bulrush. Populations of both species likely benefit and reach higher densities than they would alone. Because of the impact of the hogs on the hammock community and the unique nature of the bulrush patches, this mutualism is likely central to the functioning of this entire system. The potential existence of this mutualism was an unanticipated finding of the study.

The islands, with the greater density of hogs than the nearby mainland, are thus the destination of the majority of hog-mediated nutrient deposition. The islands have

soils richer in P, K, and N than the mainland soils, potentially indicating a sustained movement of nutrients by hogs from marshes into the terrestrial island soils. Artificial tilling to mimic rooting disturbance did not have a detectable lasting effect on plant tissue nutrient content, but exclusion of the hogs quickly reduced the nutrient content of the island biomass to mainland levels. Exclusion of hogs on the mainland did not affect levels of nutrients in the plant tissue. Even though the hog nutrient deposition is by some measures modest (1-11% of the atmospheric deposition in this area), these experiments demonstrate that hog deposition is biologically significant because the concentrations of nutrients in the herbaceous biomass depend on differences in hog abundance and access. Comparisons with typical plant nutrient levels reveal that these N and P are likely to be limiting in this system but K is abundant in both the soils and the plant tissues. Thus, the study reveals that hogs are able to indirectly alter plant nutrient content.

The nutrient transport by the hogs appears to be fairly short-range, less than 300 m with movement of nutrients to the closer islands surrounded by marsh far outweighing movement to the slightly more distant mainland (400-500 m). Based on the favoritism the hogs show the islands compared to the mainland, and given the stable isotope results and color phenotypes, there seems to be very little long-distance movement of the hogs from the coast inland and therefore nutrient transport distances are short. Indeed, the hog subpopulation that occupies the coast seems quite distinct from that found even a short distance inland. Therefore, the Feral Hogs acting as exotic generalists move nutrients as predicted based on general anthropogenic patterns of disturbance: short-range, inter-habitat transport with net flows into refuge areas from

feeding areas, but with little reason to expect large-scale, long-distance nutrient transport.

All of these ecological processes play out in landscapes modified by human impacts. In the Florida system, Feral Hogs are an introduced exotic freed from the potential regulation of their numbers by an almost extirpated top predator, the Florida Panther. However, it is important to recognize that there is a diversity of human cultures and this diversity impacts their relationships with ecosystems and influences to a greater or lesser extent the overall patterns of anthropogenic impacts on biotic systems. The final portion of this dissertation has explored the cultural context of anthropogenic impacts. A root of the diversity of human interactions with their environment is a culture's perception of the Great Divide. This division between Human and Nature, and therefore between wilderness and cultural space, is fundamental to the way people perceive reality. Though the character of that division and its universality in human cultures has been long debated, the division is inherent to self-awareness as a species and the creation of cultural space. In spite of differing emotions towards, emphasis on, and valuations of wilderness among cultures, diverse examples suggest that there is a basal universal wilderness concept, but with substantial and consequential variation among its many incarnations.

This concept of course varies among cultures and one obvious aspect that differs is the archetypical wilderness envisioned by a people. An archetypical wilderness is one viewed in a given culture as the ideal or ultimate wilderness. Readings of German, Irish, and Korean folktales show that, traditionally, German culture viewed the forest as the archetypical wilderness and Korean culture viewed mountains as the archetypical

wilderness, while no wilderness archetype could be detected for Irish culture. An analysis of protected area names in the same three cultures showed similar patterns with German protected areas having largely forest-derived names, Korean protected areas having mountain-derived names, and the prevalence of habitat types in Irish protected area names being correlated with those in Irish folk tales. The fact that the German archetype was based on land cover and the Korean archetype was based on topography led to very specific expectations for the landscape use patterns for each culture. Because deep wilderness should be avoided for development, an archetypical wilderness should be especially avoided and developed from the edges. Because land cover is easily changed compared to topography, topography should more severely delimit Korean cultural areas than German ones.

Landscape-level analyses were carried out to test this hypothesis. The expectation was satisfied in the land use patterns in Korea and Germany with respect to ruggedness and relative elevation: Korea had a more conservative and stricter decision rule with regards to development of rugged areas and more predictable elevational transitions from civilization to wilderness, consistent with a reluctance to develop a mountain wilderness archetype. Of course, Korea and Germany have very different agricultural systems, with topography being much more important in the type of wet-paddy agriculture favored in Korea. Therefore, urban development was examined with respect to the same ruggedness index and elevational transects. Because Germany does not have large cities in mountainous areas, the largest non-East Asian cities were used from around the world.

Korean cities had similar patterns to all of Korea while non-East Asian cities hemmed in by mountains were variable but similar to Germany, implying that culture, not agriculture plays a major role in patterns of land development. This is particularly powerful in showing the impact of wilderness archetypes as a culture that needs flat agricultural land can be expected to be *less* likely to build cities in the valuable lowlands and instead use uplands for urban development. This is not what is observed in Korea.

Anthropology has a long history of inclusion of environmental variables (such as habitat type/biome) in understanding human cultures and their development. Ecology, for its part, while often recognizing the profound influences that humans often have on biotic communities and ecosystems, has tended to either ignore anthropogenic influences altogether or treat them as givens without examining humanity as an ecological force in and of itself with broad rules and patterns that are followed in spite of the vast diversity of human cultures and impacts that can alter the details and thus some of the practical ramifications of anthropogenic influences on the biosphere.

Unfortunately, remaining ignorant of human behavior and patterns of impacts is no longer a realistic option for ecologists. On the one hand, there are practically no ecosystems available for study that are completely free from human influence. On the other hand, anthropogenic degradation of the Earth's ecosystems is severe enough that preservation of biodiversity and ecosystem functioning increasingly demands that anthropogenic impacts be understood and mitigated. While the Great Divide may be a primary character of human perception, in many ways it is being unintentionally broken down by the growing dominance of anthropogenic impacts and must be crossed

conceptually in the ecological and conservation sciences in order to deal with the effects of increasing human population density and global biotic degradation.

APPENDIX A  
SUPPLEMENTARY INFORMATION FOR CHAPTER 2

Although larger vertebrates form the focus of Chapter 2, many of the anthropogenic community effects discussed in the paper have been shown in a diverse range of taxa. For example:

**Plants**

- Generalist plants have increased over time in British upland habitats because of anthropogenic nutrient enrichment and disturbance (Smart et al. 2005).
- Generalist competitive (i.e., those that are dominant in high-nutrient areas) plant species have increased with time in a Belgium urban area at the expense of specialist stress-tolerators (Van der Veken et al. 2004).

**Invertebrates**

- Anthropogenic simplification of seafloor habitats impacts habitat specialists more than generalists (Thrush et al. 2006).

**Insects**

- Fragmentation had negligible effects on insect habitat generalists (Bender et al. 1998).
- Narrow habitat specialist and dietary specialist insects are especially prone to anthropogenic extinction (Dunn 2005).
- Fragmentation and urbanization favor generalist insects and especially reduce predator and parasitoid insects (Gibb & Hochuli 2002).
- Omnivorous insects are the least sensitive to a desert-urban gradient (McIntyre et al. 2001).
- Carabid beetle specialists get smaller and the generalists more common moving towards the urban end of an urban-rural gradient (Ishitani et al. 2003).
- Butterfly generalists do better with the novel foods and changes in urban areas than specialists (New & Sands 2003).
- Ants are the dominant predator in cities but vertebrates are the dominant predators in rural areas (Wetterer 1999).
- Spillover of insect generalist predators from agricultural lands to wildlands can depress their prey's numbers (Rand & Louda 2006).

- Generalist insect predators get more abundant and more important in impacted landscapes but specialists are reduced (Rand & Tscharrntke 2007).
- The number of generalist butterfly species actually increased in smaller fragments (perhaps because they were drawn in from the matrix) while specialist species increased with habitat patch size (Steffan-Dewenter & Tscharrntke 2000).
- A simplification of insect food webs with fewer interactions dominating the webs in modified habitats even though there was a retention of species diversity, however the most common parasitoid was more specialized in modified habitats (maybe because its preferred prey is more abundant so was more focused on than expected) (Tylianakis et al. 2007).
- Smaller fragments have fewer monophagous insects (Zabel & Tscharrntke 1998).
- Generalist bee and wasp species were not sensitive to urbanization (Zanette et al. 2005)

### **Crustaceans**

- Generalist exotic crustaceans dominate streams in developed areas (Brasher et al. 2006).

### **Fish**

- Generalist exotic freshwater fish dominate streams in developed areas (Brasher et al. 2006).
- Reef fish generalists were more successful after coral disturbance than specialists (Feary 2007).

### **Reptiles**

- Reptile habitat specialists were more likely to go extinct on islands (Foufopoulos & Ives 1999).
- But see Attum et al. (2006): lizard desert specialists are favored compared to generalist with human desertification because they are adapted to the desert extremes that are exacerbated by desertification.

### **Mammals**

- Fragmentation had negligible effects on mammal habitat generalists (Bender et al. 1998).
- There is an increase in generalist mammalian mesopredators, far more exotics in cities, and ants are the dominant predator in cities but vertebrates are the dominant predators in rural areas (Wetterer 1999).

- Raccoon Dogs in agricultural areas have lower activity levels than mountain individuals and individuals using concentrated resources like garbage and shoreline have small home ranges (Saeki et al. 2007).

### **Birds**

- Fragmentation had negligible effects on bird habitat generalists (Bender et al. 1998).
- Exotic and generalist birds are more common in disturbed areas (Acevedo & Restrepo 2008).
- Urban birds have broader environmental tolerances (Bonier et al. 2007).
- High human density rural areas have more habitat generalist bird species because of less native habitat, more roads, and more fragmentation (Boren et al. 1999).
- In France, birds responded more negatively to fragmentation and disturbance the more habitat specialized they were (Devictor et al. 2008).
- Increase in exurban density favored some generalist and reduced specialist birds (Fraterrigo & Wiens 2005).
- Generalist avian nest predators are more common in urban areas (Jokimäki 2000).
- Specialist birds are negatively associated and generalists positively associated with forest edges, showing the effect of fragmentation (Jones et al. 2000).
- Crows and ravens have smaller home ranges and higher reproduction with access to anthropogenic food sources, some travel 10's of km to get anthropogenic food (Marzluff & Neatherlin 2006).
- Generalist birds increase at the expense of specialists through time in an urban park (Bergen et al. 1998).

APPENDIX B  
SUPPLEMENTARY FIGURES FOR CHAPTER 3



Figure AB-1. An example of the exclosures used in the study. The exclosures are 4 m x 4 m, built from 3' hog wire fencing, and supported with metal U-posts, wooden stakes, and convenient trees.

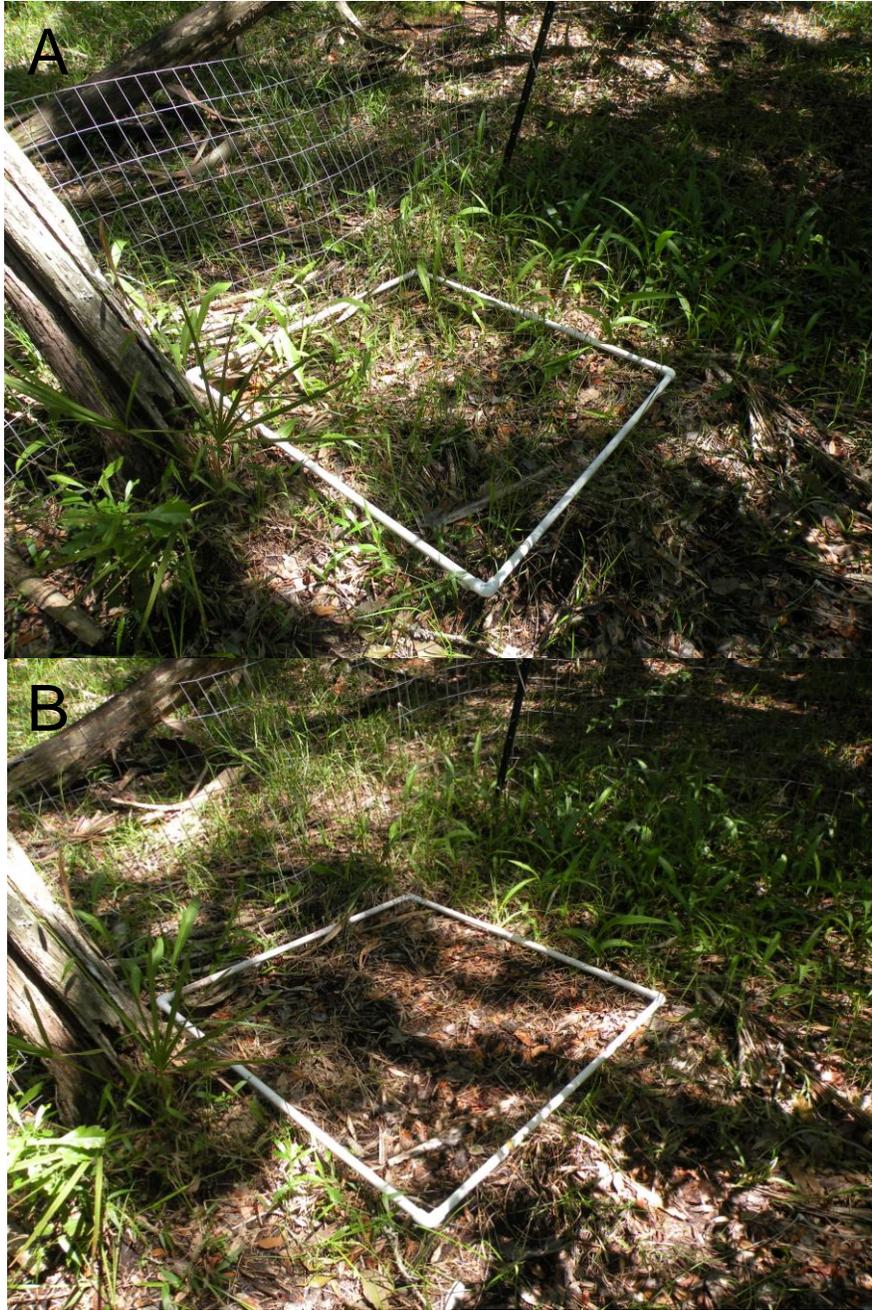


Figure AB-2. Collection of the herbaceous biomass. A 1 m x 1 m quadrat was placed randomly in one of the 16 square meters contained within each plot (A). All living herbaceous biomass was collected within the quadrats (B) with the exception of woody stems and Poison Ivy.



Figure AB-3. The effects of hog exclusion on the herbaceous community of the coastal hammock in the Lower Suwannee National Wildlife Refuge after 3.5 years were frequently visually striking.

## APPENDIX C FECAL DECOMPOSITION STUDY FROM CHAPTER 4

An attempt was made to estimate nutrient deposition based on fecal deposition rate based on an observed fecal decay rate. Unfortunately, this method produced unreasonably low estimates of hog density (on the order of 1/100 km<sup>2</sup>) and nutrient deposition (below). This failure could have been due to a bias in fresh feces found and monitored. While one specimen was noted to decay beyond recognizability in a single day, most specimens were likely found after several days, biasing the subsequent results by excluding quickly decomposing feces. Additionally, the sample size was necessarily small as fresh feces were in high demand for genetic work. The details are included here for completeness.

### **Methods**

The rate of fecal decay was established by marking fresh piles and noting when they had decayed beyond recognition. The date of decay was defined to be the midpoint between the last positive observation and the observation of disappearance. Because there was no evidence of change in fecal load among seasons, the deposition rate was considered to be equal to the decay rate.

Estimated fecal nutrient deposition rates were estimated using the observed fecal decay rate, the measured fecal loads (number of 'piles') on the islands and the mainland, the measured fecal nutrient content, and the measured weight of the fecal samples. Because nutrient deposition occurs through urine in addition to feces, N, P, and K deposition through urine was estimated based on calculated fecal nutrient deposition and the proportions of N, P, and K in domestic hog nutrient budgets excreted in the feces and in urine (Kephart & Sherritt 1990; Sands et al. 2001).

## Results

Fecal decay had a linear function with 50% decay at 471 days (Figure AC-1), which equates to a deposition rate of 3.4 fecal piles/100 m<sup>2</sup>/year on the islands and 0.5 fecal piles/100 m<sup>2</sup>/year on the mainland. The average weight of a fecal pile was 122 g ±12 SE (n = 39). The average N, P, and K content of hog feces, and estimated nutrient deposition rates for the islands and coastal mainland are given in Table AC-1.

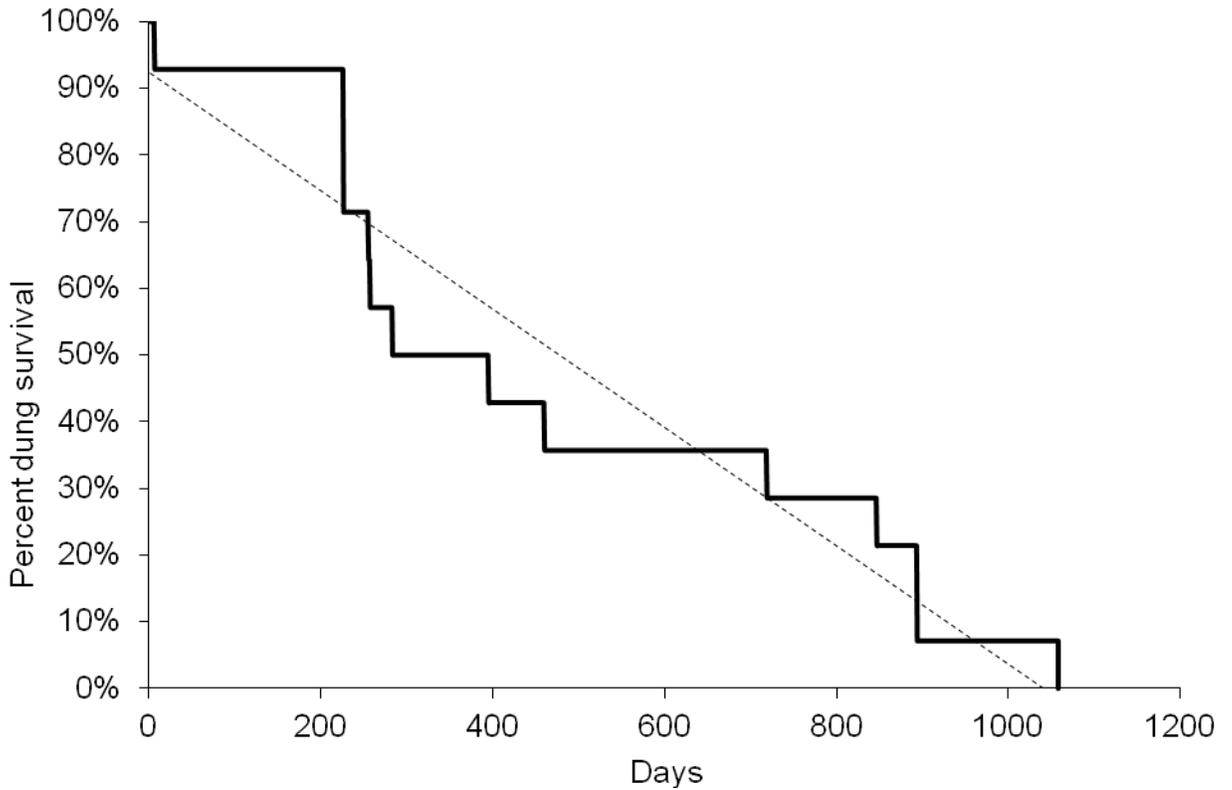


Figure AC-1. Feral Hog fecal decay in the coastal hammock of the Lower Suwannee National Wildlife Refuge (n = 14). The trend line is dashed.

Table AC-1. Calculated nutrient (N, P, K) deposition rates on the island and mainland coastal areas by Feral Hogs in the Lower Suwannee National Wildlife Refuge.

Nutrient	% of feces <sup>1</sup>	Fecal deposition (g/100 m <sup>2</sup> /year)		Urine:Feces ratio <sup>2</sup>	Urine deposition (g/100 m <sup>2</sup> /year)		Total deposition (g/100 m <sup>2</sup> /year)	
		Island	Mainland		Island	Mainland	Island	Mainland
N	0.42 ±0.04 <sup>3</sup>	1.75 ±0.73	0.28 ±0.12	2.75 ±0.45	4.80 ±2.75	0.77 ±0.45	6.55 ±2.85	1.05 ±0.46
P	0.17 ±0.02	0.70 ±0.30	0.11 ±0.05	0.54 ±0.09	0.38 ±0.19	0.06 ±0.03	1.08 ±0.35	0.17 ±0.06
K	0.14 ±0.01	0.56 ±0.23	0.09 ±0.04	3.25 ±0.16	1.83 ±0.76	0.30 ±0.12	2.40 ±0.80	0.39 ±0.13

<sup>1</sup>By wet weight

<sup>2</sup>The ratios of the amounts of the nutrients excreted through urine and feces based on hog nutrient budgets (Kephart & Sherritt 1990; Sands et al. 2001)

<sup>3</sup>Standard error

APPENDIX D

DELINEATIONS OF SAMPLING AREAS FOR CHAPTER 6

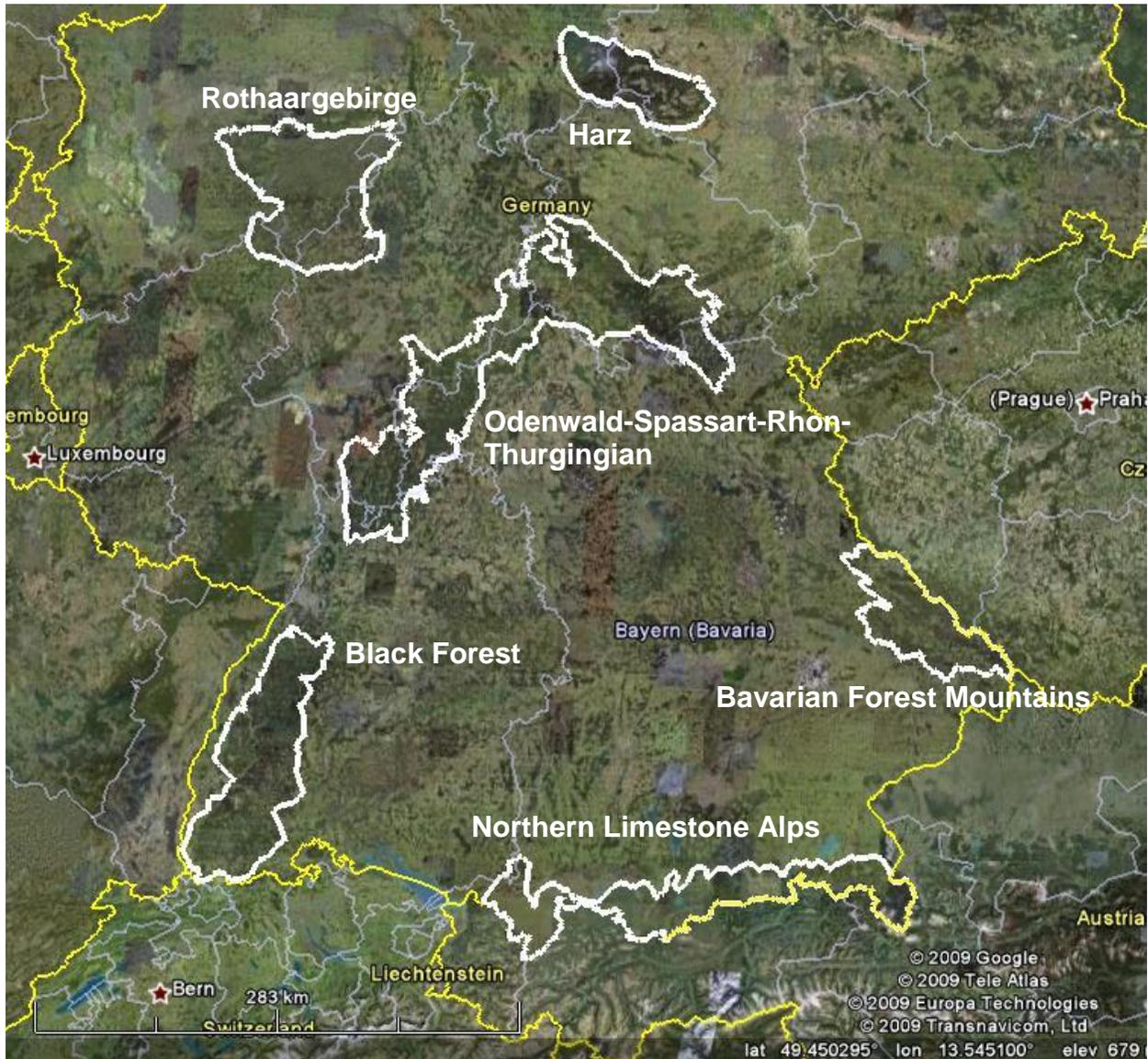
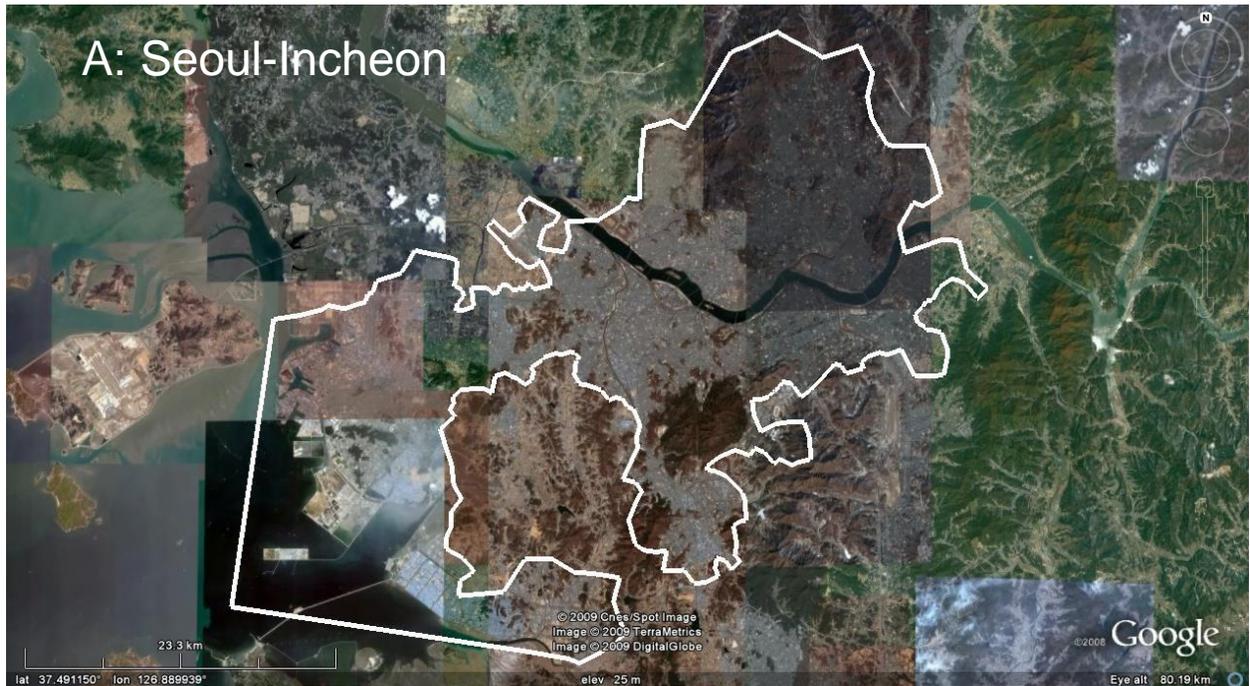
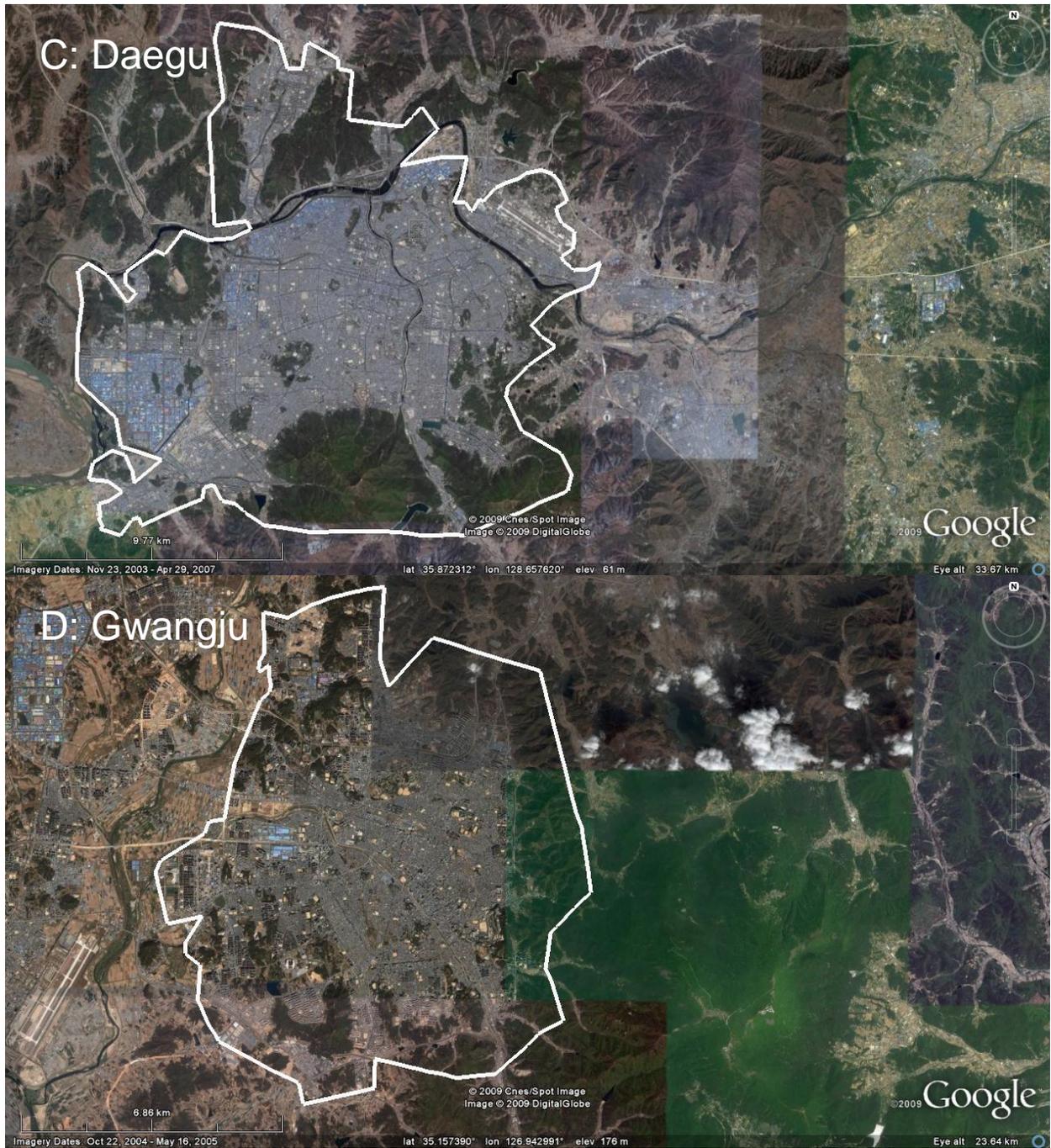


Figure AD-1. The mountainous areas in Germany (outlined in white) used for the ruggedness indices and civilization-wilderness border transects. (© 2009 Google, © 2009 Tele Atlas, © 2009 Europa Technologies, © 2009 Transnavicom, Ltd.)





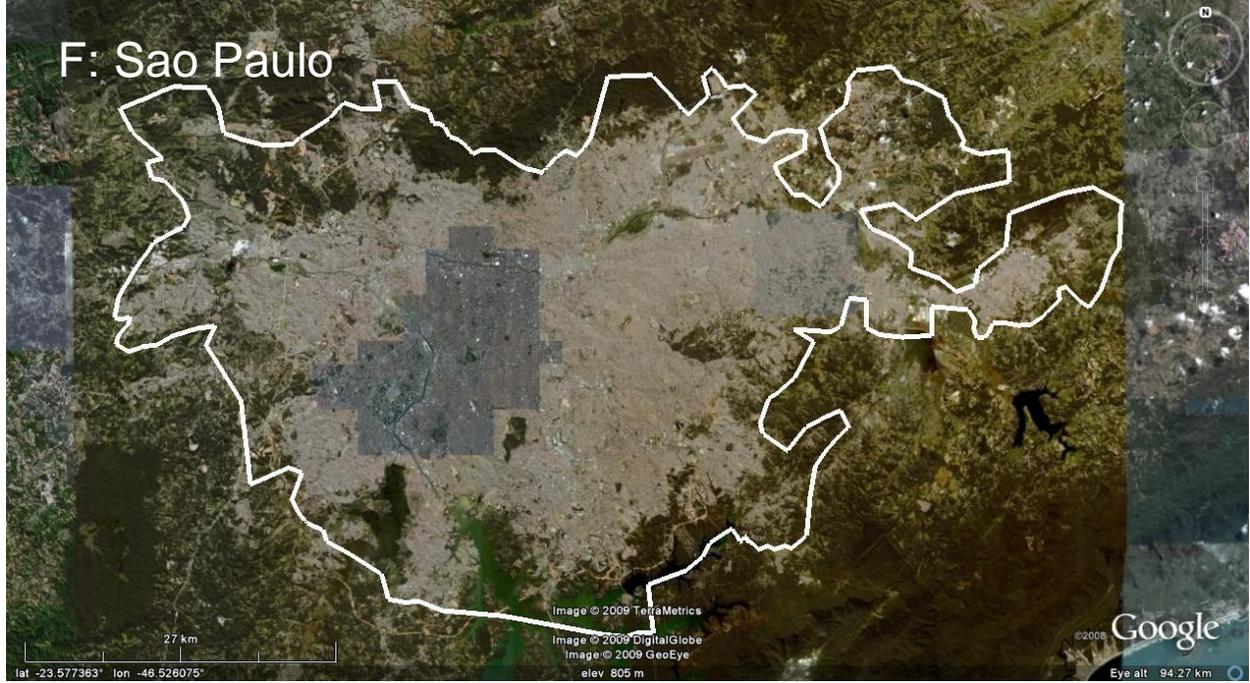
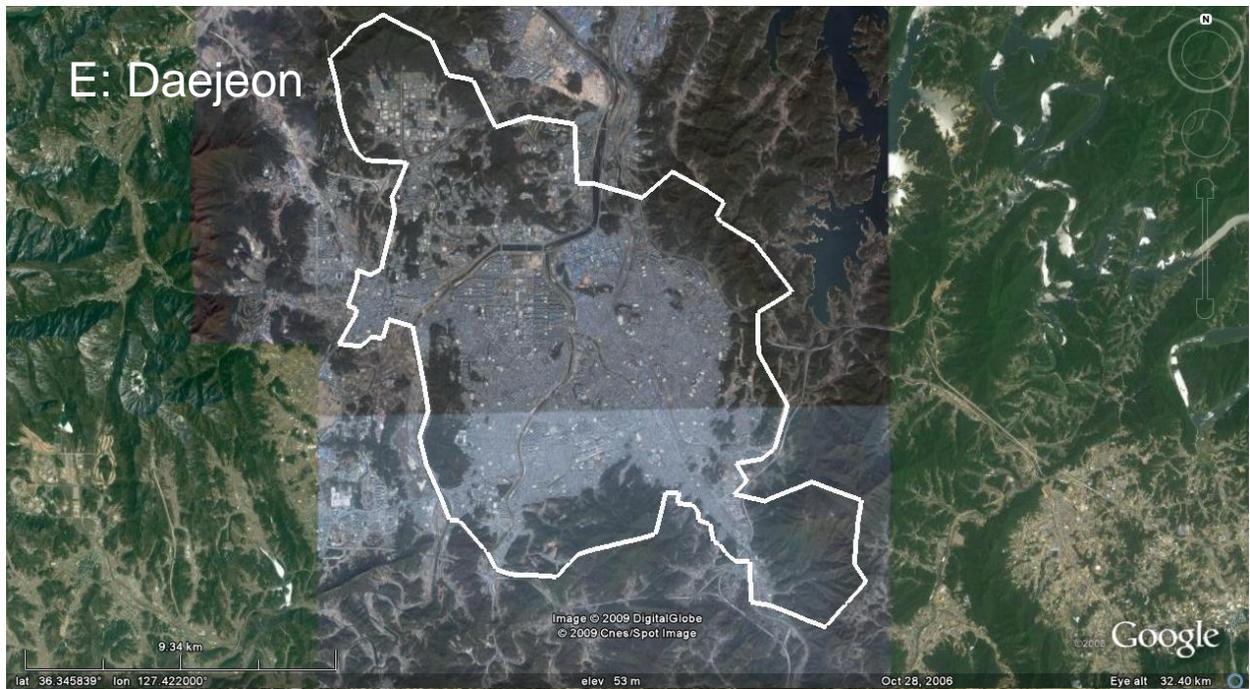






Figure AD-2: Urban areas used for comparisons of ruggedness indices and civilization-wilderness border transects. A) Seoul-Incheon (© 2009 Cnes/Spot Image, Image © 2009 TerraMetrics, Image © 2009 DigitalGlobe), B) Busan (© 2009 Cnes/Spot Image, Image © 2009 GeoEye, Image © 2009 DigitalGlobe, Data © 2009 MIRC/JHA), C) Daegu (© 2009 Cnes/Spot Image, Image © 2009 DigitalGlobe), D) Gwangju (© 2009 Cnes/Spot Image, Image © 2009 DigitalGlobe), E) Daejeon (© 2009 Cnes/Spot Image, Image © 2009 DigitalGlobe), F) Sao Paulo (Image © 2009 TerraMetrics, Image © 2009

DigitalGlobe, Image © 2009 GeoEye), G) Mexico City (Image © 2009 GeoEye, © 2009 Cnes/Spot Image, Image © 2009 DigitalGlobe), H) Los Angeles (Image U.S. Geological Survey, Image © 2009 DigitalGlobe, Data U.S. Navy), I) Istanbul (Image © 2009 DigitalGlobe, Data U.S. Navy, © 2009 Cnes/Spot Image), and J) Rio de Janeiro (Image © 2009 TerraMetrics, Image © 2009 GeoEye, Image © 2009 DigitalGlobe, Data SIO, Data NOAA, Data U.S. Navy, Data NGA, Data GEBCO).

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## BIOGRAPHICAL SKETCH

Cedric O'Driscoll Worman received an excellent elementary school education from the Minnesota public school system (wandering the forests, mountains, and deserts of North America with his family did not hurt either) and attended North Hollywood High School Magnet for Biological and Mathematical Sciences. He earned his Bachelor of Science at Iowa State University with specializations in restoration ecology and mammalian behavior. After graduation he joined the Peace Corps and was sent to Uganda where he learned more than he really wanted to. Before entering graduate school, he taught in and explored Korea. He procured his MSc. in zoology at the University of Florida by studying frugivorous monkeys and their habitat use and nutritional ecology. In the spring of 2012, he received his Ph.D. in biology from the University of Florida for the work described here.