AVIAN GUANO AS A NUTRIENT INPUT TO CLIFF – FACE ECOSYSTEMS IN WESTERN NORTH CAROLINA

A Thesis
by
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Abstract

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Terrestrial cliff-face ecosystems are unique habitats that harbor diverse vegetational communities and an array of animal species. However, fundamental processes such as nutrient cycling in cliff-face ecosystems remain poorly understood. Cliff-face vegetative communities receive some nitrogen through atmospheric deposition, but few other nutrient-linkages have been explored. Seabirds are a well-established vector of nitrogen subsides between marine ecosystems and coastal cliffs, and I document a similar nutrient transfer between highly productive forest ecosystems and nutrient-poor terrestrial cliffs. Common ravens (*Corvus corax*) and peregrine falcons (*Falco peregrinus*) are vagile forest-dwelling raptor species that frequently nest on cliffs in the southern Appalachians. Like seabirds, they excrete nitrogen-rich guano at cliff nest sites, subsequently increasing nitrogen (N) availability below nesting sites. This study investigates a fundamental ecosystem process on cliffs, nitrogen cycling, while also exploring a potential link between terrestrial forest and cliff-face ecosystems in western North Carolina.

I compared levels of N on the cliff surface between paired vertical transects with and without nesting or roosting activity. To measure the community effects of a potential nitrogen subsidy, I compared vascular plant, bryophyte and lichen diversity between the paired transects. Ammonium levels were higher on transects with raptor nests or roosts than on the control transects ($p<0.05$). My data also indicate differences between vegetation community composition below nests and on adjacent areas on control transects ($p<0.05$). For instance, three lichen species that are commonly found below bird perches, *Xanthoria candelaria, Physcia caesia,* and *Caloplaca citrina* were identified on nest transects within the present study. *Xanthoria* and *Physcia* species are eutrophic lichens, and are often indicators of high nitrogen levels in ecosystems. Eutroph presence indicates that nitrogen levels below raptor cliff nests are elevated enough to cause vegetation community composition shifts.

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Dedication

May your trails be crooked, winding, lonesome, dangerous…May your mountains rise into and above the clouds. May your rivers flow without end ... where storms come and go as lightning clangs upon the high crags, where something strange and more beautiful and more full of wonder than your deepest dreams waits for you — beyond that next turning of the canyon walls.

-Edward Abbey, Desert Solitaire

We cannot move without vibrating the waters, sending into the world the consequences of our desires. The hawk embodies these spreading waves, and the marvel of its flight startles us into paying attention. Our embeddedness is given a magnificent, tangible form: here is our evolutionary kinship splayed out in the fanning wing; here is a solid, physical link to the north woods and the prairies; here is the brutality and elegance of the food web sailing across the forest.

-David Haskell, The Forest Unseen

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Foreword

The research presented in Chapter 2 of this thesis will be submitted to the scientific journal *Castanea*, and has been prepared in accordance with the submission guidelines for the journal. Chapter 1 provides an introduction to the field of cliff research and offers background information that puts Chapter 2 into context.

The author sampling a control transect in 2014 on Snake Mountain, North Carolina.

Chapter 1: The Study Of Cliff-Face Ecosystems

Biodiversity

Although cliffs are ancient geologic formations, the study of cliff-face ecology is a relatively new field. Cliffs in the southern Appalachians have persisted for millions of years through climate fluctuations and repeated glacial advance and retreat cycles (Whittaker 1956, Walker 1987, Skinner et al. 2004). The ecosystems on cliffs are often glacial refugia, places where organisms have found refuge from the pressure of climactic fluctuations (Walker 1987). Cliffs in the southern Appalachians are home to a handful of glacial relict, endemic, and rare species (Smith 1998, Boggess 2013, Harkey 2013). These unique ecosystems are worthy of further research and investigation, especially in the face of current climate change and encroaching anthropogenic disturbances (Larson et al. 2000, Hill 2009).

Cliffs support distinct communities of lichens, plants and animals. However, cliff systems have been historically avoided by ecologists, or pegged as geologic formations rather than ecosystems. The challenging and time-consuming nature of studying cliff-face biota may have contributed to the relative paucity of ecological research on cliffs (Larson et al. 1999). Many ecologists have simply lumped cliff vegetation under the umbrella of the rock outcrop vegetational community. Even in relatively recent vegetation inventories of areas in the North Carolina mountains, including the cliff-lined Linville Gorge Wilderness, rock outcrop communities were documented but vertical cliffs were ignored (Wiser et al. 1996, Newell and Peet 1998, Smith 1998).

Vertical cliff ecosystems are different from horizontal rock outcrops. A suite of abiotic drivers unique to the vertical environment influences the vegetational community structure of cliff-face ecosystems. Major abiotic drivers include the surface heterogeneity of the rock substrate, aspect of the cliff, slope, and height of the cliff (Smith 1998, Larson et al. 2000). Within the last 20 years, pioneering research on cliffs has revealed the unique traits that clearly separate cliff communities from the rock outcrop communities (Smith 1998, Larson et al. 1999, Larson et al. 2000, Hill 2009). Due to their isolated vertical nature, cliff species are typically released from much of the intra- and interspecific competition pressure that species in adjacent forest ecosystems experience (Larson et al. 2000, Boggess 2013). Cliffs can thus shelter a great number of high-light, high-stress specialist species that can be endemic to cliff ecosystems (Colas et al. 1997, Larson et al. 2000, Harkey 2013). Similarly, many abiotic factors unique to vertical cliffs can determine vegetational distributions. Cliff ecosystems are clearly different from the adjacent forested horizontal ecosystems, however they are much more poorly understood. Recent research has attempted to better recognize the factors that affect cliff-face flora and fauna.

Recent cliff investigations have been conducted primarily by the Cliff Ecology Research Group (CERG) in Guelph, Ontario and the southern Appalachian Cliff Coalition (SACC) at Appalachian State University in Boone, North Carolina. Kelly et al. (1992) discovered ancient northern white cedars (*Thuja occidentalis* L.) growing on the Niagara Escarpment in Ontario aged up to 1,032 years old. In subsequent research, Larson and colleagues continued to highlight the importance of cliffs as climactic refuges for plant and animal species (Larson et al. 1999, Larson et al. 2000, Matthes et al. 2000). Gary Walker led some of the first efforts to study cliffs in the southern Appalachians, supporting the idea of cliffs as natural refuge ecosystems (Walker 1987). Walker (1987) found that the glacial disjunct populations of ancient *Thuja occidentallis* on cliffs contained higher genetic diversity than did their main-range relatives in the Northeastern U.S. and Canada. The glacial refugia phenomena allows for unique stress-tolerant species to exploit the cliff-face niche free of competition from forest-dwelling species (Walker 1987, Boggess 2013).

Subsequent studies of cliffs in North Carolina, Tennessee, Virginia, and Kentucky by the SACC have revealed rare, endangered, or disjunct species (Smith 1998, Ballinger 2007, Boggess 2013, Harkey 2013). A survey of the Cumberland Gap and the White Rocks Cliff System on the Cumberland Plateau escarpment found a disjunct lichen assemblage, *Cladonia pocillum* (Ach.) O.J. Rich) and three rare or state-listed plants; *Melampyrum lineare* Desr. var. latifolium, *Dicchanthelium aciculare* (Desv. Ex Poir) Gould & C.A. Clark and *Rhododendron carolinianum* Rehder (Ballinger 2007, Harkey 2013). Boggess (2013) also found the disjunct lichen, *Cladonia pocillum*, residing on cliffs at the Big South Fork Recreation Area, along with other rare species such as *Vittaria appalachiana* Farrar & Mickel, *Cynodontium schisti* (Web. & Mohr) Lindb., and *Carex cumberlandensis* Naczi, Kral & Bryson. Nepal (2010) found ancient individuals of *Juniperus virginiana* L. and living on cliffs in the Cumberland Plateau region of the Appalachians. These distinct assemblages of glacial relict, rare or endangered species underscore the importance of cliff-face ecosystems located in the Southern Blue Ridge Escarpment, Valley and Ridge, and Cumberland Plateau provinces of the southern Appalachian Mountains.

Terrestrial Cliff Nutrient Dynamics

Southern Appalachian cliff ecosystems have been consistently revealed as unique, biodiverse habitats. However, many critical ecosystem processes, such as nutrient cycling, remain understudied. At the same time, the SACC at Appalachian State University and the CERG at The University of Guelph have continued to recommend further research addressing ecological problems unique to cliff-face biota and their habitat (Smith 1998, Larson et al. 2000, Hill 2009). The study of nutrient dynamics and other important ecosystem process on cliffs is critical, especially in the face of impending environmental threats.

The most critical known threats to cliff-face ecosystems include habitat fragmentation, disturbance, and recreational development (Nuzzo 1996, Brambilla 2004, North Carolina Wildlife Resources Commission 2005, Kuntz and Larson 2006, Kelly and Larson 1997, Boggess 2013). Air pollution in the form of excess nitrogen (N) deposition may also pose a threat to southern Appalachian cliff-face ecosystems in the future. Land use change and the growth of regional cities increase atmospheric N deposition even in remote alpine areas (Loppi 2014, Jovan et al. 2012, Pinho et al. 2012) Although atmospheric deposition maps for the 2013 year show relatively low levels of NH_4-N and NO_3-N deposition in the southern Appalachians (NADP 2014), cliffs harbor many species that are potentially sensitive to elevated N levels. Lichens, the most abundant form of vegetation in cliff ecosystems, can absorb nutrients directly into their cortex and are often sensitive to atmospheric pollutants and have been frequently used as air-quality bioindicators (Brodo et al. 2001, Jovan et al. 2012, Loppi 2014). Oligotrophic and mesotrophic lichens typically display negative physiological effects and eventually die, while eutrophic lichens are tolerant and can thrive in the presence of elevated N (Jovan et al. 2012). Thus, elevated atmospheric

N deposition will likely depress oligotrophic and mesotrophic lichen diversity in cliff faces, especially in areas of high surface heterogeneity where nutrients accumulate (Purdy unpublished data). Due to their sensitivity to N, the absence or reduced presence of these lichens could be indicators of elevated N inputs on cliffs. Little else is known about how atmospheric deposition and other potential threats, such as global climate change, could impact cliff-face ecosystems in the southern Appalachian mountains (North Carolina Wildlife Resources Commission 2005, Boggess 2013, Purdy unpublished data).

In order to properly manage impending threats to cliff ecosystems, it is important to first understand how cliff-face nutrient dynamics operate without the addition of elevated atmospheric N. Only a single study has addressed nitrogen cycling in cliff-face ecosystems specifically (Purdy unpublished data), although Larson et al. (2000) provide some information regarding potential N-inputs to cliff systems. In a cliff ecosystem lacking soil, the flow of nitrogen is different than in a terrestrial forest nitrogen cycle (Larson et al. 2000). Because of the general lack of soil for plants to take root in, lichens are the most abundant form of vegetation on a cliff (Larson et al. 2000). They are the primary colonizers of rock, and thus play an important role in the cliff ecosystem N-“cycle”. As plants host mycorrhizal symbionts in a forest ecosystem, some lichens host cyanobacteria symbionts that fix N_2 from the atmosphere (Brodo et al. 2001) Atmospheric deposition (both dry and wet) of NO_x and NH_x to the cliff face is likely absorbed by saxicolous lichens (Johansson et al. 2012, Jovan et al. 2012) Cliff lichens also likely absorb N in the form of NH_4^+, NO_3^- and DON directly across their outer cortex membrane (Nash 1996, Johansson et al. 2011) in water runoff from the cliff-top forest ecosystem (Larson et al. 2000, Purdy unpublished data). Lichens may also directly absorb dissolved organic N (DON) compounds into their cortex (Nash 1996). Rock lichen communities likely leach NH_x, NO_x, and DON in rain events to (Nash 1996). Lichens lower on the vertical cliff face could potentially absorb these forms of N as well, creating a nutrient-uptake spiral similar to nutrient spiraling observed in terrestrial stream ecosystems. Cliff plants can also uptake NO_3^-, but likely only if soil is available.

Atmospheric deposition (either deposited directly on the cliff as dry deposition, absorbed and metabolized by saxicolous lichens, or carried in cloudwater as wet deposition) and runoff from cliff-top forest communities have been suggested as potential nitrogen inputs to cliff-face ecosystems (Larson et al. 2000, Purdy unpublished data). Other nitrogen inputs, such as those from animals, are undocumented in terrestrial cliff systems. In terrestrial forest ecosystems, animals play an integral role in the nitrogen cycle. Many animals inhabit terrestrial cliffs, but their roles in the flow of nitrogen in a terrestrial cliff-face ecosystem are largely unknown. Marine cliffs, in contrast, have been frequently investigated in the context of animal inputs to the cliff nitrogen cycles (Anderson and Polis 1999, Barrett et al. 2005, Wainright et al. 1998). These marine examples indicate that animals could have a significant role in the nitrogen cycle of a terrestrial cliff ecosystem.

Nutrient Dynamics of Marine Cliffs

There are many situations in which nutrient transfer occurs between dissimilar ecosystems. Nitrogen, in particular, is a key component in global nutrient cycling between aquatic, marine, and terrestrial ecosystems. While N cycling has only recently been investigated on cliffs here in the southern Appalachians, N transfers across ecosystem boundaries are well documented and exist in a number of systems. As previously discussed, N can be deposited on cliffs via the atmosphere or by runoff from the forest above (Purdy unpublished data). However, it is unknown whether there are other major N inputs to cliff-face vegetational communities. Many animal species utilize cliff ecosystems, including arthropods, gastropods, reptiles, mammals, amphibians, and cliff-dwelling birds (Lee and Spofford 1990, Matheson and Larson 1998, Herrel 2001, Millan et al. 2003, Pleszewski 2003, Brambilla 2004, New Hampshire Fish and Game Department 2005, NCWRC 2005, Hooper 2012). It is likely that these cliff dwelling fauna provide N to cliffs by excreting feces and urine, and by dying on the cliffs. Matheson and Larson (1998) suggest that avian communities may be involved in seed dispersal to cliffs and with nutrient cycling in cliff ecosystems. However, to date no studies have addressed potential avian nutrient inputs in terrestrial cliff systems. The most intensively studied examples of avian N input to cliffs are those involving ocean birds transferring marine N to sea-cliff ecosystems (Anderson and Polis, 1999, Barrett et al. 2005, Ellis 2005, Craig et al. 2012, Wainright et al. 1998), and it is possible that similar processes of avian nutrient transfer could exist on southern Appalachian cliff systems in western North Carolina.

Nitrogen is transferred from nutrient-rich marine ecosystems to adjacent relatively nutrient-poor ecosystems (rocky islands, rock outcrops, maritime cliffs) via seabirds and mesocarnivores like coyotes who consume marine prey (Mizutani and Wada 1988, Wainright et al. 1998, Anderson and Polis 1999, Barrett et al. 2005, Ellis 2005, Craig et al. 2012, Żółkoś et al. 2013, Brown 2014). Seabirds are typically vagile, cosmopolitan species in many orders within the class Aves: Sphenisciformes (penguins), Procellariiformes (albatrosses, petrels, shearwaters, storm-petrels, diving-petrels), Pelecaniformes (pelicans, boobies, cormorants, frigatebirds, tropicbirds, anhingas), Charadriiformes (shorebrids, skuas, gulls, terns, skimmers, auks, auklets, puffins), and Ciconiiformes (herons, egrets, night-herons) (Ellis 2005, Żółkoś et al. 2013). Marine birds often form large rookeries on rocky islands, maritime cliffs, and in estuaries. Marine bird rookeries can drastically alter the neighboring ecosystems and the areas in which they are located with nutrients from their guano (Mizutani and Wada 1988, Wainright et al. 1998, Anderson and Polis 1999, Barrett et al. 2005, Ellis 2005, Craig et al. 2012, Żółkoś et al. 2013).

Birds ingest fish or macroinvertebrate marine prey, fly to their terrestrial nesting colony, and excrete waste in the form of uric acid ($C_4H_4N_4O_3$) (Wainright et al. 1998). Rapid microbial mineralization and oxidation converts uric acid into ammonium (NH_4^+) and then nitrate (NO_3^-) which fertilizes vegetation near nesting colonies (Mizutani and Wada 1988, Wainright et al. 1998, Anderson and Polis 1999, Barrett et al. 2005, Craig et al. 2012). Ammonium also volatizes into ammonia (NH_3) and can be blown to terrestrial ecosystems downwind of nesting colonies, further transporting the marine-derived nitrogen subsidy (Wainright et al. 1998). Marine cliff ecosystems and rocky outcrops are dependent on guano subsidies to the extent that some plants and lichens there are deemed “ornithocoprophilous” (literally, “bird-dung-loving”) and arthropod communities shift from plant feeders to dung feeders when new rookeries are colonized (Mizutani and Wada 1988, Brodo et al. 2001, Craig et al. 2012, Żółkoś et al. 2013). Marine birds clearly provide a trophic link from productive ocean ecosystems to arid islands devoid of nutrients (Anderson and Polis 1999, Rajakaruna et al. 2009) and the nutrients from marine avian guano support both plant and animal life cycles on these islands (Mizutani and Wada 1988, Odasz 1994, Wainright et al. 1998, Anderson and Polis 1999, Barrett et al. 2005, Fukami et al. 2006, Maron et al. 2006). No studies have yet attempted to map a similar potential nutrient transfer to terrestrial cliff-face ecosystems surrounded by forests. Just like their marine relatives, raptor species in nutrient-rich terrestrial forest ecosystems may transport N to nutrient-poor cliff ecosystems by excreting guano at their nest and roost sites on the cliff face.

A diverse group of animals including birds, reptiles, mammals, amphibians, and invertebrates inhabit cliff-face ecosystems in eastern North America (Matheson and Larson 1998, Herrel 2001, Millan et al. 2003, Pleszewski 2003, NCWRC 2005). While terrestrial cliff systems host less dense avian communities than do those of marine cliff rookeries, a significant number of avian species inhabit or utilize the cliff ecosystem (Matheson and Larson 1998, NCWRC 2005). Common ravens (*Corvus corax* L.), great-horned owls (*Bubo virginianus* Gmelin), turkey vultures (*Cathartes aura* L.), black vultures (*Coragyps atratus* Bech.), rock doves (*Columba livia* Gmelin), red-tailed hawks (*Buteo jamaicensis* Gmelin), peregrine falcons (*Falco peregrinus* Tuns.), and American kestrels (*Falco sparverius* L.) are all documented terrestrial cliff-nesters in eastern North America (Scott et al. 1977, Craig and Craig 1984, Lee and Spofford 1990, Johnston 1992, Kirk and Mossman 1998, NCWRC 2005). Even eastern bluebirds (*Sialia sialis* L.), eastern phoebes (*Sayornis phoebe* Lath.), and cliff swallows (*Petrochelidon pyrrhonota* Viel.) are known to occasionally use rock crevices for nest sites (Scott et al. 1977, Brown and Brown 1995, Weeks and Harmon 2011).

Raptors and other large bird species who regularly utilize cliff crevices for nesting or roosting purposes are the focus of this study. Their nests likely provide the most significant nitrogen input to cliff-face vegetational communities out of all potential cliff-nesting birds in western North Carolina. Peregrines were nearly extirpated from North Carolina largely due to the use of DDT in the twentieth century (Pearson 1942, Hickey 1969, Boynton and Currie 1993, Augspurger and Boynton 1998), but were re-introduced through a successful captive breeding program (NCWRC 2005). In 1999, they were removed from the United States Federal Endangered Species List, however their recovery remains closely monitored. The North Carolina Wildlife Resource Commission works with land management agencies (United States Forest Service, National Parks, NC State Parks) in North Carolina to compile nesting site data annually (Lee 1990, Dzialak et al. 2006, NCWRC 2005). Peregrine falcons almost solely nest on cliffs, although there are records of the birds nesting in large old-growth trees before the majority of them were logged (Hickey 1969, Scott et al. 1977). Common ravens, although not technically considered raptors, are large passerines that often utilize cliffs crevices or very tall trees as nest sites (Marzluff and Angell 2005). Turkey vultures and great-horned owls are considered cavity nesters, but do not always nest in cliffs. (Scott et al. 1977, NCWRC 2005). When encountered on a cliff, turkey vulture nests can be very noticeable due to the smell of carrion, however they are often concealed to protect young (Scott et al. 1977). Thus, common ravens and peregrine falcons are probably the most consistent cliff-nesters in western North Carolina. Also, both species of cliff-nesting birds' abilities to move between forest and cliff ecosystems highlights a potential undocumented nutrient link between dissimilar ecosystems.

Vegetational Response to Avian Guano

Marine studies of avian-facilitated nutrient linkages often cite specific ornithocoprophilous species as indicators of elevated N. Similarly, a recent study documenting air pollution in the Los Angeles basin used specific epiphytic lichens as indicators of increased atmospheric N deposition (Jovan et al. 2012). Indicator species can be important tools to identify vectors of nutrient subsidies in ecosystems (Jovan and McCune 2006). On cliffs, the dominant vegetation type is lichens (Larson et al. 2000). Previous studies of saxicolous lichens near bird perches in marine systems have revealed that certain species of eutrophic lichens often appear near areas supplemented by elevated N (Mizutani and Wada 1988, Brodo et al. 2001, Craig et al. 2012, Żółkoś et al. 2013). One of the eutrophic indicator genera commonly observed in air quality studies and near dung-enriched areas included is *Xanthoria*. *Xanthoria* is a genus of bright orange lichens that is often cited as occurring near pack rat middens, bird perches, and areas of elevated atmospheric N deposition (Wooton 1991, Mitton 2006, Riddell et al. 2011). Local land managers who are attempting to locate peregrine falcon nests often cite the "orange lichen" as anecdotal evidence of bird perches or nesting activity (John and Dale 2007, Kelly 2014, Pope 2015).

On terrestrial cliffs, areas of high guano concentration or "whitewash" are typically concentrated directly below the raptor nests. Whitewash areas are often observed to be associated with swaths of orange lichen (Pope, 2015). In fact, local biologists Jesse Pope of the Nature Conservancy and Christine Kelly of the North Carolina Wildlife Resource Commission use orange lichen to locate peregrine falcon and raven nests (Kelly 2014, Pope 2015). The species of these swaths are unknown, largely because evidence of orange lichens as raptor nest indicators is anecdotal. However, saxicolous orange lichens thriving in eutrophic habitats, especially near bird-dung, are often identified as members of the genus *Xanthoria*, *Candelaria*, and occasionally, *Caloplaca* (Armstrong 1984, Ashton 1978, Davies et al. 2007, Greenfield 1992, John and Dale 2007, Wootton 1991, Armstrong and Welch 2007, Jovan et al. 2012, Żółkoś et al. 2013). Eutrophic lichens living under raptor nests on cliffs could potentially indicate N-driven lichen community shifts (Gaio-Oliveira et al. 2005, Mitton 2006, Armstrong and Welch 2007, Julig et al. 2012)

In studies documenting the impact of seabird guano on rocky islands or maritime cliffs, orange *Xanthoria* and *Caloplaca* species are commonly observed near areas of whitewash or downwind of nesting colonies where volatile N may be carried (Ashton 1978, Wootton 1991, Gaio-Oliveira et al. 2005, Armstrong and Welch 2007, Hansen 2012, Żółkoś et al. 2013). A third genus, *Physcia*, often occurs along with *Xanthoria* near areas of bird-guano on arctic or maritime rocks (Ashton 1978, Wootton 1991, Gaio-Oliveira et al. 2005, Armstrong and Welch 2007, Hansen 2012, Żółkoś et al. 2013). Both of the latter genera are often categorized as eutrophic (nitrophilous) lichens (Greenfield 1992, Davies et al. 2007, Jovan et al. 2012, Hansen 2012, Żółkoś et al. 2013). The grey *Physcia* is often documented in a band or fringe along the edge of large swaths of orange *Xanthoria* near maritime bird perches (Wootton 1991).

Orange lichens in the genus *Xanthoria* also often occur around nitrogen rich dens of the pika (*Ochotona spp.*) and on rocks near pack rat (*Neotoma* spp.) middens (Brodo et al. 2001, John and Dale 2007, Eversman 2007, Mitton 2006, Eversman 2014). Hikers, naturalists, and conservation organizations in Colorado anecdotally use these flagship orange lichens as an indicator of pika presence in sensitive alpine areas (Mitton 2006). The presence of orange lichens on alpine rocks cautions hikers and trail workers that pika or marmot may be denning there, and that they should not be disturbed (Mitton 2006, Colorado Fourteeners Initiative 2010).

Species shifts in lichen communities near dung-enriched areas can be explained by varying nutrient or pH tolerance in lichens (Jovan et al. 2012). Moderately nitrogen tolerant mesotrophic species and sensitive oligotrophic species cannot tolerate high-nutrient conditions, and are often eliminated near areas of high N (Armstrong 1984, Brodo et al 2001, Jovan et al. 2012). Elevated nutrients can upset the balance of photobiont and mycobiont symbionts inside some lichens (Johansson et al. 2012). Differing physiological responses to increased nutrient input usually are the cause of lichen species shifts (Johansson et al. 2011, Johansson et al. 2012). Thus, community shifts in areas of elevated N are often due to foliar damage among lichen species, as is often the case for vascular plants and bryophytes (Krupa 2003, Johansson et al. 2012).

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Laban Swafford inspects an area below a peregrine falcon nest site at Buzzard's roost.

Chapter 2: Avian Guano As A Nutrient Input To Cliff-Face Ecosystems In Western North Carolina

Abstract

The nitrogen cycle is an important component of all ecosystems, and often links dissimilar ecosystems, yet it remains under-investigated in terrestrial cliff-face ecosystems. Plants and lichens on the cliff face receive some nitrogen (N) from atmospheric deposition or cliff-top runoff, but no other N inputs have yet been explored in these systems. Here, I document a nutrient transfer to terrestrial cliffs via cliff-nesting birds in North Carolina. To explore the effects of a potential N subsidy, I compared vegetational community composition on vertical transects on the cliff face with and without nests and the potential N subsidy to cliff-face ecosystems by attaching ion exchange membranes to the rock face on vertical transects with bird nests and on adjacent control transects without nests. My results revealed greater differences in the vegetation communities between guano and control transects than among sites within a treatment. I also found higher levels of NH_4-N below bird nests than on control transects, but large variability in NO_3-N levels prevented me from finding similar differences for this form of N. Overall, I document a significant nutrient subsidy to terrestrial cliff ecosystems that links relatively nutrient-poor cliff ecosystems to surrounding highly productive forest ecosystems via avian inputs from guano. The presence of an avian-

mediated nitrogen subsidy is evidence that animals do play a role in the flow of nitrogen on cliff-face ecosystems. This suggests that other cliff-dwelling animals may also function as part of the cliff-face nitrogen cycle.

Introduction

Cliff ecosystems encompass a unique habitat home to a biodiverse group of plant, animal, and lichen species, many of which are rare or endemic (Walker 1987, Colas et al. 1997, Larson et al. 2000, Boggess 2013, Harkey 2013). Historically, cliffs were not considered unique ecosystems, and were avoided by ecologists (Curtis 1959, Larson et al. 1999). However, recent research has led ecologists to recognize the importance of cliff ecosystems and the need for their conservation (Walker 1987, Kelly et al. 1992, Kelly and Larson 1997, Larson et al. 2000, Matthes et al. 2000). Cliff-dwelling species are governed by a suite of abiotic pressures unique to the vertical environment such as surface heterogeneity, aspect of the cliff face, and slope of the cliff determine vegetation distributions. Cliff ecosystems are largely untouched by the disturbances that affect the surrounding forests (e.g., logging, mining, development, land-use change) (Larson et al. 1999, Larson et al. 2000) However, these habitats face potential threats to their biodiversity including atmospheric pollution, development, and anthropogenic disturbances (Nuzzo 1996, Larson et. al. 2000, Brambilla 2004, North Carolina Wildlife Resource Commission 2005, Boggess 2013). Recently, ecologists have recommended further study in order to understand how to best manage and conserve cliff ecosystems (Nuzzo 1996, Larson et. al. 2000, Brambilla 2004, NCWRC 2005, Hill 2009, Boggess 2013).

Cliffs have recently been revealed as distinct biodiverse ecosystems and many fundamental ecosystem processes on cliffs remain poorly understood. For example, terrestrial cliff-face nitrogen (N) cycling has been explored in a single study (Purdy unpublished data). Cliff-face plants and lichens can receive N from atmospheric deposition or cliff-top runoff, but other nitrogen inputs to cliff vegetation are unknown (Purdy unpublished data). Purdy (unpublished data) found N to have an important role in cliff-face ecosystems. High nitrogen levels were found in areas of high surface heterogenity where soil typically collects (Purdy unpublished data). Nitrogen was also found to drive competition in vegetative communities, causing lower biodiversity at higher levels of N (Purdy unpublished data). Purdy's research indicates that N may be an important driver of vegetational community compostion in terrestrial cliff-face ecosystems.

Studies of vegetation on maritime cliffs and rocky islands reveal that elevated levels of N from seabird rookeries drives vegetational communtiy composition (Anderson and Polis 1999, Barrett et al. 2005, Ellis 2005, Rajakaruna 2009). For instance, in areas of high N availability, ornithocoprophilous (bird-dung loving) plants and lichens have adapted to depend on the subsidy (Anderson and Polis 1999, Ellis 2005, Rajakaruna 2009).

Avian communities utilize terrestrial cliff-face ecosystems for nesting, roosting or perching. Matheson and Larson (1998) recorded a variety of species perching on cliffs or in cliff-face vegetation. A number of cavity-nesting birds occaisionally nest in rock crevices on the cliff, while certain species specialize in nesting on cliff ledges (Hickey 1969, Hooper 1977, Scott et al. 1977, Craig and Craig 1984, NCWRC 2005). In North Carolina, common species of avian cliff-nesters include the common raven (*Corvus corax*) peregrine falcon (*Falco peregrinus*), turkey vulture (*Cathartes aura*) and occaisonally, great horned owls

(*Bubo virginiana*) (Scott et al. 1977, NCWRC 2005, Kelly 2014). Matheson and Larson (1998) found that terrestrial cliffs had an influence on bird community diversity, and suggest that birds utilizing terrestrial cliffs may play a role in nutrient cycling and seed dispersal. As in marine systems, it is possible that guano and debris from bird nests and roosts could be an important N input to the terrestrial cliff-face nitrogen cycle. The present study documents a potentially important nutrient input from the avian community to terrestrial cliff-face ecosystems in western North Carolina. Cliff-nesting raptors are vagile animal species whose potential N inputs may link forest ecosystems to terrestrial cliffs. As the nitrogen cycle is a vital process in any ecosystem, documenting nutrient inputs to the cliff-face nutrient cycle is an important step towards understanding the functioning of cliff-face ecosystems.

The current study has three main objectives: 1) to determine if there is more mineral nitrogen below cliff bird nests than in areas on the cliff face where bird nests are absent, 2) assess potential vegetational community differences between areas with and without bird nests on terrestrial cliffs, and 3) to examine whether any changes in vegetational communities correlate with the amount of nitrogen added.

Methods

Study Area Description

The study area spans most of western North Carolina, from Pilot Mountain in the northeast to Chimney Rock in the south and Buzzard's Roost in the west (Figure 1). Most of the sites were located within the Blue Ridge physiographic region. Pilot Mountain, a metamorphic monadnock remnant of the ancient Sauratown mountain chain, was the only site located in the Piedmont physiographic region of North Carolina. Four of the sites occurred inside the Pisgah National Forest, three sites inside North Carolina State Parks, and one site on private land.

Forest types observed around the sites varied from mixed oak-hickory in lower elevations to spruce-fir at the highest elevation sites. Some hemlock and beech stands occurred at sites that were near water or on north-facing slopes, and occasional pine-oak groves occurred at drier rocky areas at the edge of the cliffs. Common plants observed near cliff sites were *Vaccinium* spp., *Clethra* spp., *Rhododendron* spp., *Azalea* spp., and *Viburnum* spp.

Geology of the Study Area

A cliff's regional and local geomorphology is important to the abiotic components of cliff plant community structure. Cliff flora experience substantially more intimate contact with the bedrock of a cliff than do other horizontally-oriented ecosystems (even rock outcrops) because soil formation is so minimal (Larson et al. 2000).

The region of this project largely consists of metamorphic rock formed during the Precambrian period (4.6 billion – 542 million years ago) (Skinner et al. 2004) (Figure 1). The Blue Ridge Physiographic region consists of a large mountain chain that was created during the Alleghenian orogeny 200-300 million years ago (Skinner et al. 2004) when continental plate collisions caused a large uplift, exposing older metamorphosed rock from the Precambrian period and forming the Appalachian Mountains. Much of the Precambrian rock that created the cliffs where the study sites are located is among the oldest in the region and the world (Skinner et al. 2004).

Field Collection Methods

Study Site Selection

Cliff study sites were chosen based on three criteria: 1) recent presence of nesting raptors, 2) accessibility, and 3) safety. Raven, peregrine falcon, turkey vulture, great-horned owl, and other raptor species' nests were located through citizen science data and records from land managers or biologists. Recent avian studies attempting to cover a large area or time span cost-effectively often use citizen science data (Sullivan et al. 2009, Harris et al. 2013). Nest searches for large raptors are extremely time-intensive, and would have proved difficult to execute over the large study area and rugged terrain. Many ravens may also nest in large trees, so a nest search encompassing a raven's home range would be inefficient and potentially ineffectual. To protect their nests from disturbance, peregrine falcon home ranges are closed during breeding season (January 15-August 15) when nest searches typically occur. Ravens and other raptors sometimes share these home ranges, making their territories inaccessible to nest searches during the breeding season. The closures and time intensive nature of nest searches for large raptors necessitated the use of citizen science data and land manager records.

The peregrine falcon nest site records were obtained through Chris Kelly of the North Carolina Wildlife Resources Commission (NCWRC) and the North Carolina Natural Heritage Commission site occurrences map. To locate specific nest sites of other birds, local rock climbers and birders were polled between October 2013 and May 2014. I emailed contacted approximately 150 local rock climbers through an active email list (the Watauga Climber’s Club) maintained by experienced climber and longtime study-area resident Michael Trew. Many users of this email group are also active members of climbing stewardship organizations such as the Carolina Climbers Coalition, Access Fund, and American Alpine Club. I also polled the High Country Audubon Society, a dedicated organization of local bird watchers in the study area. Lastly, I queried rangers and biologists at any of the land management agencies in my study area where birds had either historically nested on cliffs, or where recent cliff-nesting activity was likely: Pisgah National Forest Ranger District, Nantahala National Forest Ranger District, Gorges State Park, Chimney Rock State Park, Pilot Mountain State Park, Moore’s Wall, South Mountains State Park, Grandfather Mountain State Park, Mount Jefferson State Natural Area, Elk Knob State Park, New River State Park, and the National Park Service at the Blue Ridge Parkway.

I gathered and compiled all reports generated by land managers and citizens and confirmed nesting activity at all reported sites (excluding those within the peregrine falcon closures) between October 2013 and June 2014. If no evidence of nesting activity was found, I discarded those sites. Citizen-generated sites harboring old raptor nests, but no visual confirmation or fresh evidence of recent nesting activity (detailed below), were not included in the study. Most of my sites were located on public land and sampling permits were granted by the United States Forest Service (USFS) and North Carolina State Parks. One of my sites was reported to us by a private landowner who granted us permission to sample on his property. On one occasion, a nest site on private property adjacent to a state park was discarded due to rejection of my proposal by the land owner.

To confirm recent activity, I returned to sites where nesting material or whitewash was initially observed on the first visit. These areas were then assessed for breeding activity or visual evidence of recent nesting (new nesting material, prey remains or droppings). Due to the extremely remote nature of my sites, activity was alternatively confirmed by land managers, rangers, or skilled citizen observers in some cases. For sensitive peregrine falcon nest sites within NCWRC and USFS closures, nesting activity was confirmed via monitoring data from Chris Kelly of NCWRC for the 2014 season. For these sites, safety and access was assessed after the closures lifted in August 2014.

Next, I ranked sites based on access difficulty and safety, discarding any sites that were dangerous or extremely difficult to access. One site that was above the skill set of my research team and a professional volunteer was Looking Glass Rock in Pisgah National Forest. The site had confirmed nesting activity of peregrine falcons in 2014 and a safe approach hike. However, to actually enter the nest site required researchers to climb an extremely difficult three pitches (or rope lengths) of climbing rated A3+. This level of climbing is typically only attempted by experienced and/or professional climbers and can be dangerous even when attempted by them. I discarded Whitesides Mountain and Victory Wall in Pisgah National Forest for these reasons and also a site in the Valle Crucis gorge because it was too difficult for researchers to effectively sample. I decided not to sample at White Rocks Cliff or Grandfather Mountain due to extreme access difficulties and the sensitive nature of the ecosystem surrounding the Grandfather sites. Sampling for all sites took place after the fledging (or abandonment) of nests by all raptors between August 15 and December 5, 2014.

Sampling Procedures

At each cliff nest study site, I sampled paired transects: a “guano” transect and a “control” transect. I set up one transect at the nest site and one at an adjacent site at an average of approximately 15 m away on the cliff face with no guano or nesting/roosting evidence. When possible, I selected control transects with similar aspect, slope, and surface heterogeneity measurements to the nest transect. Rappel stations were set up by equalizing at least three natural anchors at the top of the cliff (Figure 2). Investigators rappelled to access each transect using a Petzl GriGri 2 assisted braking device with additional knot backups during collection activities (overhand knot, GriGri mule.) For extra safety, researchers were also backed up on a second static rope with a belay from the top of the cliff or with an autolocking Petzl ASAP device (Figures 3 and 4).

Transects consisting of 1 m^2 quadrats were sampled on each side of the rappel rope (one plot to the left and one to the right), along the cliff face at 3 m intervals. The number of plots sampled varied with the height of the cliff (Figure 5). Samples of vascular plants, lichens, and bryophytes were collected from paired plots along each transect beginning three meters above the nest site and continuing at 3 m intervals until reaching the cliff base (Figure 6). When possible, the edge and talus areas were also included in the sample. Aspect, slope, and surface heterogeneity were recorded in all plots. Percent cover of plant and lichen species was visually estimated within each 1 m^2 quadrat. Surface heterogeneity was visually estimated and assigned a value between one (low heterogeneity: smooth rock) and four (high heterogeneity: cracked, pocketed, or pitted rock). Aspect and slope were measured with a compass and inclinometer, respectively.

Vegetation samples were temporarily placed in paper bags or envelopes and labeled with the site and transect code. Vascular samples were transferred to a plant press in the field and identified upon return to Appalachian State University. For certain crustose lichen samples that are impossible to identify in the field, it was necessary to remove them with a hammer and chisel. In these situations, I attempted to minimize scarring and impact to the cliff. At sensitive sites that were either popular tourist attractions or climbing routes, I took photos of crustose lichens for morphotype identification. Vascular plant samples were identified to species when possible by myself and Drew Jenkins at the Appalachian State University Herbarium (BOON) using the nomenclature of Weakley (2012). Bryophyte samples were identified to species by Dr. Keith Bowman. Lichen samples were identified to species when possible, or genus, or morphotype by myself and Dr. Coleman McCleneghan at Appalachian State University using the nomenclature of Brodo et al. (2001).

Nutrient Analysis

Ion resin nutrient traps were used to measure potential nitrate ($^-$) and ammonium (NH_4^+) contributions of avian nest sites to the cliff ecosystem. The traps are made from cation and anion exchange resin sheets (AMI7001; CMI7000, Membranes International Inc., Ringwood, NJ). The sheets were cut into 5x5 cm strips and attached to the cliff face using 3M™ double-sided foam outdoor mounting tape. Previous work by Purdy (unpublished data) indicated no measurable leaching of N on to resin strips from the tape. The area of attachment on the cliff was cleaned with wire and fine bristle brushes in order to remove granular material that could inhibit adhesion.

Both a cation and anion trap were placed in each quadrat on either side of the rope at 3 m vertical intervals along each transect, beginning 1 m from the top of the cliff and directly under each nest site (Figure 7). Traps were collected after three months, and processed in the lab for NH_4^+ and $^-$ using KCl extraction and subsequent spectrophotometric analysis (Binkley 1984, Madritch and Hunter 2002). . Using data from the KCl extraction, I estimated NO_3-N and NH_4-N levels on the cliff face. For each trap, I calculated micrograms of NO_3-N and NH_4-N per cm^2 at each of the quadrats where traps were collected.

To assess community differences on the cliff face, four metrics were used: species richness and species evenness were calculated for each vegetational community type (lichen, vascular plants, and bryophytes) in each quadrat. Shannon-Weiner (H') and Simpson's Index (D) were separately calculated to estimate vegetational diversity at the plot level. The Shannon index uses both species richness and abundance in the formula:

$$\mathrm{H}' = -\sum_{i}^{R} p_i \ln p_\mathrm{i}$$

Where R is the total number of species in the population and p_i is the proportion of the number of individuals of species i compared to the total number of individuals of all species in each 1 m^2 quadrat. The Simpson's Index (D) uses the formula:

$$\mathrm{D} = (n - 1)(N - 1)$$

Where n is the total number of individuals of a particular species and N is the total number of individuals of all species in a plot. The Shannon-Weiner Index typically is used in cases where there may be a few rare species in the sample, while the Simpson's Index gives more weight to dominant species. I used both indices to attempt to account for the diverse types of vegetation communities on cliff ecosystems. There are often cases of sparse vegetation coverage with only a few species occurring in a sample, but these sample areas are often located adjacent to areas rich in diversity. All data collected from the quadrats on the left and right sides of the rope were then averaged at the plot level. After running initial descriptive statistics, data that did not meet normal distribution assumptions for parametric tests were transformed accordingly.

Statistical Methods

Permutation-based nonparametric MANOVA (PerMANOVA)

A PerMANOVA is a non-parametric distance-based multivariate analysis of variance that is well suited for non-normal or sparse ecological data (Peck 2010). I had a multivariate experimental design and data did not meet the distributional assumptions of a MANOVA. Therefore, I utilized a nested two-factor model PerMANOVA blocked by site in order to test for differences in vegetational community composition between guano and control transects (PC-ORD V6, MjM Software, Glendenen Beach, Oregon). A p value of < 0.05 was considered significant.

Paired t-*tests*

To investigate differences in N transects, I employed paired *t*-tests in SigmaPlot (Version 12.5, Systat Software, San Jose, CA). I also used paired *t*-tests to describe differences in species evenness, richness, and diversity, and percent cover for each vegetational community type between guano and control transects. A p value of < 0.05 was considered significant. Data that could not be transformed to meet normal distribution assumptions were tested using non-parametric Mann-Whitney rank-sum procedure.

Results

Effects of Bird Nests on Cliff-Face Nitrogen Levels

NH_4-N levels were higher on guano transects than on the control transects (*p* = 0.006). N levels, however, were not different between guano transects and controls (*p* = 0.24) (Figure 8). Species diversity for most vegetational communities did not change when exposed to excess bird guano, except for lichens and all vegetation considered as a whole. Species richness for lichen communities and for all vegetational communities grouped together was marginally lower on guano transects (*p* = 0.060 and *p* = 0.052, respectively). Lichens and all vegetational communities did not display differences in overall diversity, as determined from the Shannon-Weiner (*p* = 0.244; *p* = 0.248) and Simpson's Index (*p* = 0.987; *p* = 0.812). Vascular plants and bryophytes also showed no difference in biodiversity beneath bird nests, either with the Shannon-Weiner index (*p* = 0.145; *p* = 0.168) or Simpson's Index (*p* = 0.124; *p* = 0.134). Species evenness for lichen communities was higher on guano transects than on control transects (*p* = 0.024), as well as species evenness for all vegetational communities grouped together (*p* = 0.006).

Lastly, vascular plants and bryophytes also did not exhibit major changes in species richness (*p* = 0.271; *p* = 0.254) or species evenness (*p* = 0.146; *p* = 0.105). The only communities that demonstrated some difference in diversity when located under bird nests were lichens and all vegetation grouped together. These communities had higher species evenness under bird nests and marginally lower species richness. Lichens and all vegetational communities as a whole were the communities that reflected the greatest variation in community composition among guano and control sites.

The percent of organisms covering the cliff face was largely the same among guano and control transects for lichens ($p = 0.475$) and vascular plants ($p = 0.349$). Bryophytes were the only group to differ in percent cover on guano transects ($p = 0.037$), and they covered less of the rock face on guano transects than on control transects.

PerMANOVA

PerMANOVA results indicate no difference between communities on control and guano transects when all transect data was included in the analysis ($p > 0.05$). All data were subsequently truncated to two plots below the nest site on each transect to consider a local effect of guano on vegetational communities. The PerMANOVA analysis indicated significant differences in the overall species composition of vegetational communities below bird nests. Also, the results revealed a trend of differences in vegetational communities among sites (Table 1). In all cases, except for vascular plants, the guano effect was equal to or greater than the site effect. All vegetation as a group varied the most between study sites ($p = 0.0008$), while lichens and vascular plants differed marginally ($p = 0.056$). Bryophyte communities, however, were not different among study site locations ($p = 0.121$).

The effect of bird guano on the vegetation community was larger than that of site location. All vegetation grouped together ($p = 0.0008$) and lichen communities ($p = 0.003$) were different below bird nests than on control transects. Bryophyte communities changed marginally below bird nests ($p = 0.054$). Vascular plants were the only community that did not display differences between guano and control transects ($p = 0.248$). Although vascular plants did not match the overall trend, the entire vegetational community as a whole (dominated by lichens) strongly exhibited a response when exposed to bird guano. Lichens as a community were marginally less species rich and had higher species evenness underneath bird nests.

Discussion

Nitrogen Below Nests

Nitrogen levels were higher under bird nests on the terrestrial cliff faces in this study. The elevated nitrogen levels were sufficiently high to influence the vegetation community composition below nests. This evidence shows that avian inputs of N to can have important influences on the ecology of cliff-face vegetation communities in the southern Appalachians, just as marine avian rookeries do in sea cliff ecosystems.

Nutrient linkages between dissimilar ecosystems such as the one documented here are common. Maritime rookeries, for example, provide large amounts of elevated nutrients from ocean ecosystems otherwise nutrient devoid land-based island cliff ecosystems. Cliff-nesting raptors are vectors moving nitrogen from the ocean to terrestrial cliff ecosystems. Cation traps below nests on guano transects detected higher NH_4-N per cm^2 in each plot than on the control transects. Studies of marine systems have documented birds transferring significant amounts of nutrients from areas of high primary productivity in the ocean to otherwise nutrient devoid maritime cliffs and rocky islands (Wootton 1991, Anderson and Polis 1999, Barrett et al. 2005, Ellis 2005). These rookeries are typically much larger than are the raven and peregrine falcon nesting areas present in western North Carolina. However, my data indicate that these less dense terrestrial nesting areas nevertheless do make a significant nitrogen contribution to the cliff ecosystem in North Carolina.

Terrestrial cliff-nesting birds such as peregrine falcons and common ravens spend up to 6 months at their nest, between nest-building and rearing young (Marzluff and Angell 2005, NCWRC 2005). During this time, they forage for prey in forests surrounding the cliffs. They bring back prey to feed their young at the nest, and uneaten prey, feather debris, and guano contain N in the form of amino acids. Fungal or bacterial decomposers typically break down these proteins through ammonification, converting the N in the amino acids to ammonium (Bernhard 2010). Uric acid ($C_4H_4N_4O_3$) in guano is also rapidly mineralized by bacteria after it is excreted at the nest, it is first converted to ammonia, then oxidized by bacteria into nitrate (Wainright et al. 1998, Bernhard 2010). Nitrate levels were not significantly different on the cliff face under bird nests, possibly due to a high sampling error that occurred with the nitrate data, loss of traps in the field, and a naturally higher mobility of nitrate in ecosystems (Vitousek 1979). High sample error likely occurred because many of the cation and anion traps fell off for unknown reasons. Some may have been lost to storms, or local seepage on cliffs. Others appeared to have been eaten (or at least partially eaten) by animals, while others were never found. In areas of high climbing traffic, climbers likely discarded some of the traps as trash. Thus, in some locations, my nitrate data lacked sufficient geographic coverage to make any ecological inferences. In future research, the traps should be more closely monitored or removed earlier in order to avoid this problem. Alternatively, I may not have detected a difference in N levels between guano and control transects because nitrate is more mobile in terrestrial ecosystems than is ammonium. Ammonium can bind to negatively-charged cation exchange sites on clay soil particles, is more easily volatilized, and uptake of ammonium by vegetation, lichens and bacteria temporarily immobilizes it (Vitousek 1979, Dahlman 2004). While soils were largely absent from my cliff sites, the similar mechanism may immobilize ammonium on cliff faces. Lichens also tend to have an affinity for the uptake of ammonium over nitrates or dissolved organic N (Dalhman 2004). Thus, nitrate levels on cliffs may have spiked during the nesting season and subsequently were flushed from the cliff ecosystem when heavy use of the nest sites ended. In future research, if cation and anion traps could be attached to the cliff beneath active nests, differences in nitrate levels may be detected more readily. Also, further investigations of roosting areas that are used year-round may have greater potential for detecting variation in nitrate levels. Nitrates are indeed absorbed by lichens, however I did not find differences in nitrate levels below bird nests. Nonetheless, higher ammonium levels under bird nests show that terrestrial cliff-nesting birds add an N subsidy to cliff-face ecosystems, and may suggest that ammonium may be a more important form of N in determining cliff-face lichen distributions.

Higher N levels under bird nests than on adjacent control transects indicate that peregrine falcons, common ravens, and other cliff-nesting birds in western North Carolina provide a nitrogen subsidy that links terrestrial forest ecosystems to cliff-face ecosystems. Purdy (unpublished data) found that nitrogen inputs to cliff-face nitrogen cycles came largely from atmospheric deposition and from forest runoff, but he did not consider N inputs from avian sources. Lichens on the cliff-face likely take up N from runoff, the atmosphere and from cliff-nesting bird nests. Some lichens may also leach organic and inorganic N back onto the cliff face after rain events, which would create a nutrient spiral (Figure 9), leading to the loss of N from the ecosystem. N retention in cliff-face ecosystems is probably lower relative to input compared to terrestrial ecosystems because of the lack of soil retention, the low vegetational biomass and cover, and the vertical nature of the habitat. This evidence suggests that the control of the N cycle on cliff-faces fundamentally differs from that of more typical terrestrial forest ecosystems. Such differences may imply that the controls on vegetational processes also differ, and any perturbations due to abiotic stressors may exert effects in a different manner, or have more direct effects due to the low storage capabilities of cliff-face ecosystems.

If cliff-nesting birds also contribute N to the cliff-face nitrogen cycle, it is possible that other biotic and abiotic inputs to the cliff-face nitrogen cycle could exist. For instance, a diverse group of arthropods, gastropods, reptiles, amphibians, mammals, and other cavity-nesting birds dwell on cliffs (Lee and Spofford 1990, Herrel 2001, Millan et al. 2003, Pleszewski 2003, Brambilla 2004, New Hampshire Fish and Game Department 2005, NCWRC 2005, Hooper 2012) and could provide similar nutrient inputs to the cliff ecosystem by excreting feces or urine on the cliff-face and by themselves dying and decomposing (Figure 10). Abiotic interactions with the nutrient cycle in cliff ecosystems should also be considered; little research has addressed disturbance regimes such as fire on cliffs (Plezewski 2003). Fire could potentially interact with the cliff nutrient cycle by altering microbial, animal and vegetational cliff communities, and does affect cliffs in the Linville Gorge Wilderness Area (Kuppinger 2010, Lesch-Huie 2014). Anthropogenic disturbances such as cliff-top housing development and local air pollution should be further investigated for their interaction with the cliff nutrient cycle. Excess nutrient run-off from cliff-top development or from atmospheric deposition could alter cliff vegetational communities. This study documents one example of a biotic interaction with the cliff-face nutrient cycle. Cliff-nesting raptors are a vector for a nitrogen subsidy to terrestrial cliff ecosystems, but it is possible that other relationships between cliff dwelling biota and the cliff-face nutrient cycle occur.

Vegetational Community Change

In marine systems, avian guano typically has a greater effect on vegetational communities in otherwise nutrient-poor habitats than in already nutrient-rich habitats (Ellis 2005). Terrestrial cliffs are typically low-nutrient areas (Larson 2000, Purdy unpublished data) and elevated N below bird nests is likely a driver of the vegetational community differences observed there in this study. Lichens are the dominant vegetation group on the cliff-face, and they drive the variation seen when all vegetation is considered together as a group.

Lichens and all vegetation grouped were marginally less species rich and more even below bird nests, while bryophytes were marginally different. The effect of guano outweighed the effect of study site location in lichen and bryophyte communities, and was equal to the effect of site location when all vegetation was grouped together. Recent research in the field of cliff-face ecology has found large site-specific differences in vegetation (Smith 1998, Larson et al. 2000, Ballinger 2007, Hill 2009, Boggess 2013, Harkey 2013). The SACC has used the results from recent studies to recommend site-specific cliff management to conservation groups and land management agencies (Walker 2014). However, in this study, I document that the effect of cliff-nesting bird guano is at least as large as is the site effect for all communities except vascular plants. The presence of bird guano broadly affected vegetational community composition on the cliff face. In terrestrial cliff ecosystems most previous research on cliffs has found larger differences in vegetational communities among sites than within sites (Smith 1998, Larson et al. 2000, Ballinger 2007, Hill 2009, Boggess 2013, Harkey 2013, Walker 2014). Since site variation is typically large in cliff ecosystems, detection of other abiotic or biotic effects can be potentially difficulty. My finding of an effect of bird guano to cliff face ecosystems overcomes this site-to-site variation, and thus suggest that the input of N from bird nests is important to cliff ecosystems.

Vascular plants were the only community that differed more among study sites than between guano and control transects. Vascular plants did not exhibit any differences in community composition in response to the presence of bird guano. In studies of vascular plants near maritime rookeries, guano typically effects community composition, species richness and total plant biomass (Ellis 2005). The density of nesting birds in this study is much lower than that of a typical maritime rookery. Decreased nesting density, decreased temperature and increased precipitation can reduce the magnitude of the guano effect on the plant community (Ellis 2005). It is possible that vascular plants in this study did not respond to the presence of bird guano because only one pair nested at each study site, providing less guano than a large bird colony. Alternatively, temperature or precipitation may have interacted with the effect of guano nitrogen on vascular plant community composition in this study.

Additionally, vascular plant communities may not have shown an effect from avian guano because they comprised a small portion of the vegetational community in this study. In contrast, lichen communities were the most abundant community in this study, and are typically the largest component of vegetational communities on rock faces (Larson et al.

2000). Lichens also directly absorb nutrients into their cortex, while vascular plants primarily take up nutrients through their roots. Thus, vascular plants may take a longer period of time to respond to the nitrogen increase from bird guano than lichens. I lacked records for all of the raven nests, and thus could not determine the time period that each area had been exposed to elevated N from guano. Using records from the NCWRC, I could determine approximately how long peregrine falcons had used a general area for nesting. However, I did not know how long they had used the exact location of the nesting crevices that I was sampling. Thus, it was not possible to detect effects of the time period of nest establishment on vegetational communities. Perhaps future research can explore whether longer established nests will have a greater effect on the vascular plant community and vegetational community as a whole.

Lichen communities and all vegetational communities grouped together exhibited significant differences in community composition among guano and control transects. Specifically, these groups had higher species evenness (the relative abundance of species in a sampled area) and marginally lower species richness (the relative number of species present) on guano transects than on control transects. However, there were no differences in species diversity (Shannon-Weiner Index and Simpson's Index) between areas of high nitrogen under nests and low nitrogen under control transects. Higher species evenness and slightly lower species richness for lichen and all vegetational communities below bird nests are not necessarily indicators of lower biodiversity, but may imply a weak trend towards lower diversity under bird nests. It is clear that the addition of guano by bird nests affects the vegetational community, yet it is not clear exactly how it affects vegetational biodiversity.

Lichens and all vegetation as a whole exhibited differences in species evenness and species richness below bird nests, but these communities did not show a difference in percent cover under bird nests. Vascular plant communities were also not different under bird nests in respect to percent cover. Bryophytes were the only community that had lower percent cover under bird nests. Bryophytes as a community have variable sensitivities to elevated nutrients (Pitcairn et al. 2003). Some bryophyte species are bioindicators of enhanced air pollution in tandem with lichens, whereas others tolerate high amounts of N (Bobbink et al. 2002, Pinho et al. 2012). Purdy (unpublished data) did find that that lower bryophyte diversity correlated with higher nitrogen availability. It is possible that the species of bryophytes dwelling on cliffs within the study area do not tolerate elevated N. Another variable such as a change in pH due to the addition of guano could have also caused low abundance of bryophytes under nests. Our results indicating that few bryophytes persist under areas supplemented by N further reveals an impact of avian guano on the vegetational community of terrestrial cliffs.

Lichen community percent cover did not differ under bird nests, but my results did indicate differences in lichen community composition between nest and control transects. I also identified two species of known eutrophic lichens below bird nests (*Xanthoria candelaria* (L.) Th. Fr., and *Physcia caesia* (Hoffm.) Fürnr.,) (Jovan and McCune 2006, Riddell et al. 2011). A large swath of *Xanthoria candelaria* was discovered directly underneath the common raven nest at the Snake Mountain study site (Figure 11). Similarly, at Big Lost Cove 2, a band of *Caloplaca citrina* (Hoffm.) Th. Fr. and *Physcia caesia* were found underneath a raven roosting area on the guano transect. Other species of the eutrophic genus *Physcia* were observed, including *Physcia subtilis* Degel. on the Big Lost Cove 1, Pilot Mountain, and Buzzard's Roost guano transects. *Physcia* spp. were also observed on some control transects as well. Vegetational community shifts were visually apparent at other sample locations coinciding with guano presence (Figure 12). Lichens are typically divided into three categories based on their nitrogen sensitivity: eutrophic (or nitrophilic), mesotrophic, and oligotrophic. The changes observed in lichen communities under bird nests indicates that eutrophic lichens thrive directly below nests where mesotrophic and oligotrophic lichens are absent.

The discovery of large swaths of orange lichen, *Xanthoria candelaria* and *Caloplaca cintrine*, under areas enriched by guano on cliffs match anecdotal claims of orange-colored lichens as bioindicators of cliff bird nests. All three species mentioned above are also members of genera that are commonly found under bird perches on arctic, maritime, or alpine rocks. Two of the identified genera: *Xanthoria* and *Physcia*, are considered eutrophic lichens (McCune and Jovan 2006, Riddell et al. 2011). It is unclear whether orange *Caloplaca* is also eutrophic or simply coincidentally located under bird perches. No literature specifically includes *Caloplaca* as a nitrophilic lichen or air quality indicator species, however some studies mention it occurring near areas enriched by guano from arctic bird perches (Ashton 1978, Wootton 1991). Davies (2007) also describes multiple epiphytic species of *Caloplaca* and *Xanthoria* occurring in London, England, in an area of enhanced atmospheric N. Although no studies have yet specifically indicated *Caloplaca* as nitrophillic, its occurrence with *Xanthoria* in areas of high N concentrations indicates that it may be a eutrophic genus. Thus, the orange-colored lichen genera *Xanthoria* and perhaps *Caloplaca* can be used by managers as a visual tool to help locate nests of cliff-nesting birds. This information can aid subsequent conservation efforts for monitored cliff-nesting species in North Carolina such as the peregrine falcon.

Nitrogen availability influences plant and lichen community composition near large marine bird rookeries on rocky maritime islands or cliffs (Wainright et al. 1998, Anderson and Polis 1999, Ellis 2005). Nitrogen-loving species are typically found in these areas, some have even adapted to depend on bird guano (ornithocoprophilous vegetation) (Rajakaruna 2009). Elevated bioavailable nitrogen from the atmosphere and from bird dung can decrease diversity in these areas, as well as decrease vegetational diversity in cliff ecosystems (Hauck 2011, Craig et al. 2012, Purdy unpublished data). On guano transects, along with finding higher levels of NH_4-N than on control transects, the PerMANOVA results revealed vegetational community differences between guano and control transects. Lichen community composition was also different between guano and control transects, while bryophyte communities were only marginally different. These results indicate that cliff-nesting raptor nests impact vegetational community composition on southern Appalachian cliffs. Lichens as a community category displayed the largest difference between areas with and without guano, likely driving the variation seen in the grouped "all vegetation" category. Lichens are the most abundant community on cliffs, and often the first community to shift when exposed to elevated nutrients, and are often used as indicators of excess atmospheric nitrogen (Larson et al. 2000, Jovan 2012). Lichen community response below bird nesting is likely due to their nitrogen sensitivity. Thus, albeit on a smaller scale than around large marine rookeries, terrestrial cliff nests drive vegational community differences locally through the addition of nitrogen.

Conclusion

In recent years, multiple studies have revealed cliff systems to be distinct ecosystems worthy of conservation and further exploration, however several basic ecosystem processes in cliff ecosystem remain poorly understood. One important process, nutrient cycling, has only recently been considered in the context of cliff-face ecosystems. This study documented one interaction within the nitrogen cycle of a terrestrial cliff ecosystem. Cliff-nesting birds are an integral part of the unique cliff ecosystem; they provide a nitrogen input to the cliff-face nutrient cycle and affect vegetational community composition on the vertical cliffs. While the interaction of cliff birds and plants via nitrogen in guano is well known for marine systems, this study documents a similar pathway in terrestrial cliff systems. The importance of cliff-nesters to local plant life on cliffs should be considered in conservation efforts for terrestrial cliff systems. Cliff-nesting raptors typically spend a large part of the year nesting on cliffs (February-August for some peregrines), and continue to perch on cliff ledges throughout the year (Kelly 2014). Many of the perches or roosts provide alternative nitrogen inputs, although smaller than those of their nesting areas. Birds excreting guano while utilizing the cliff face may also act as a mechanism of seed dispersal from the surrounding forests to the cliff face. The avian community is not just a temporary visitor to cliffs; terrestrial avian cliff-nesters are a dynamic component of the cliff-face ecosystem.

Cliffs are complex ecosystems, subject to many of the same cycles and ecological pressures as traditional “horizontal” ecosystems. This study documents an interaction within cliff-face ecosystems in the southern Appalachians that could potentially exist in other cliff ecosystems. Cliffs worldwide remain under-investigated; yet probably exhibit a wealth of diverse relationships among organisms. Cliff enthusiasts, rock climbers, land managers, and future cliff ecologists should consider cliffs as a unique vertical ecosystem, linked to the surrounding forests by the trophic pathway of cliff-nesting raptors.

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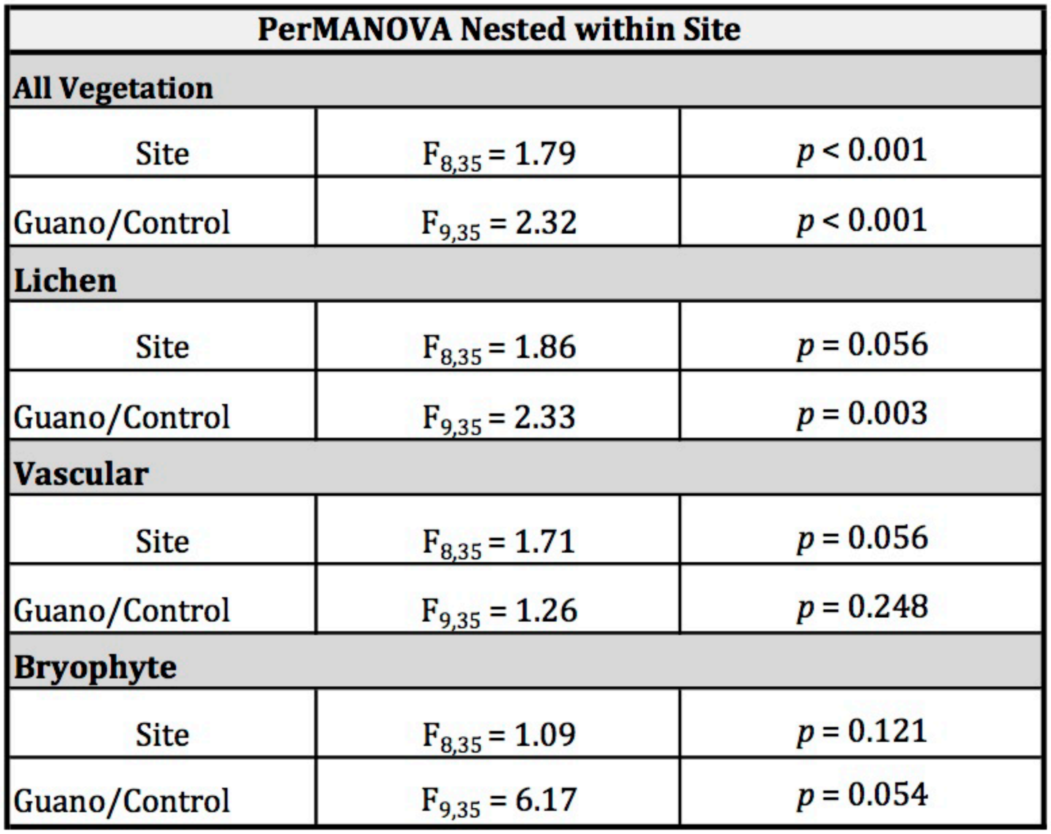
Nestling common raven (*Corvus corax*) at the Snake Mountain study site, 2014.

(Photo: Doug Blackford, HCAS.)

Tables



PerMANOVA Nested within Site		
All Vegetation		
Site	$F_{8,35} = 1.79$	$p < 0.001$
Guano/Control	$F_{9,35} = 2.32$	$p < 0.001$
Lichen		
Site	$F_{8,35} = 1.86$	$p = 0.056$
Guano/Control	$F_{9,35} = 2.33$	$p = 0.003$
Vascular		
Site	$F_{8,35} = 1.71$	$p = 0.056$
Guano/Control	$F_{9,35} = 1.26$	$p = 0.248$
Bryophyte		
Site	$F_{8,35} = 1.09$	$p = 0.121$
Guano/Control	$F_{9,35} = 6.17$	$p = 0.054$

Table 1. Results of the PerMANOVA indicates variation between guano transects and control transects, and among study sites.

Figure Legends

Figure 1. Overview Geologic map of study area, including points of all sampled study sites. The map also includes rock type and topography. Legends available in Appendix 7.

Figure 2. Laura Boggess checks two anchors for equalization before adding a third, demonstrating the safety of a three-point anchor system**.**

Figure 3. Researchers on rappel setting up a sample plot (Boggess 2013).

Figure 4. The author on rappel at Table Rock with an extra belay for back-up.

Figure 5 & 6. Diagram of the sampling design (Smith 1998). Photograph of 1 m^2 quadrat paired plots used on either side of the rappel line (Boggess 2013).

Figure 7. Cation and Anion traps below a nest on a face plot at Buzzard's Roost.

Figure 8. NH4-N levels were higher on guano transects than on the control transects, but NO_3-N levels were not significantly different, and had higher sample error.

Figure 9. Diagram of the hypothesized terrestrial cliff N-cycle.

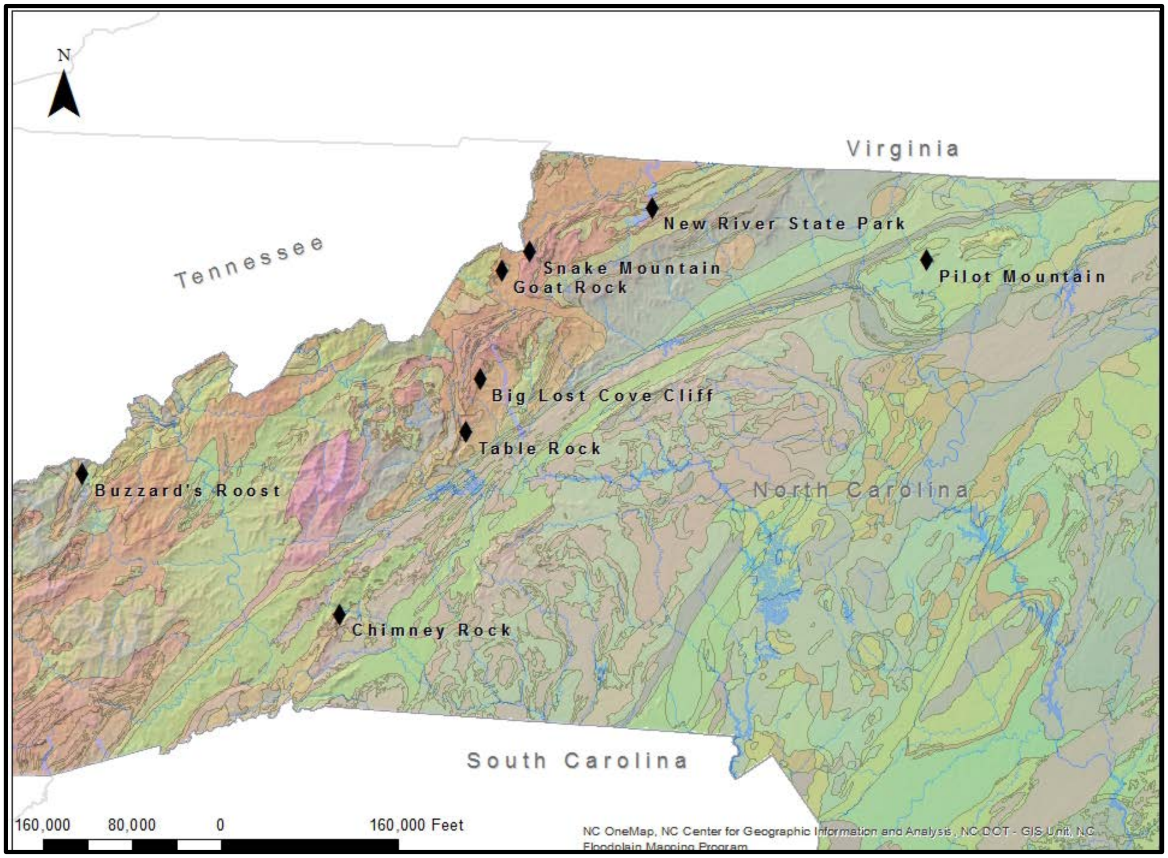
Figure 10. Evidence of mammalian use of cliff-face crevices and cracks: a rodent den located on the sheer cliff face of Chimney Rock, approximately 150 feet below the cliff edge and 150 above the talus.

Figure 11. The orange eutrophic lichen *Xanthoria candelaria* thriving underneath the *Corvus corax* nest at Snake Mountain.

Figure 12. Visual change in lichen community exhibited at Chimney Rock on a popular perch site often used by peregrine falcons nesting nearby (*Falco peregrinus*). This site was sampled as the guano transect for Chimney Rock.

Figures

Figure 1.



NC OneMap, NC Center for Geographic Information and Analysis , NC DOT - GIS Unit, NC Floodplain Mapping Program

Figure 2.

Figure 3.

Figure 4.

Figure 5 & 6

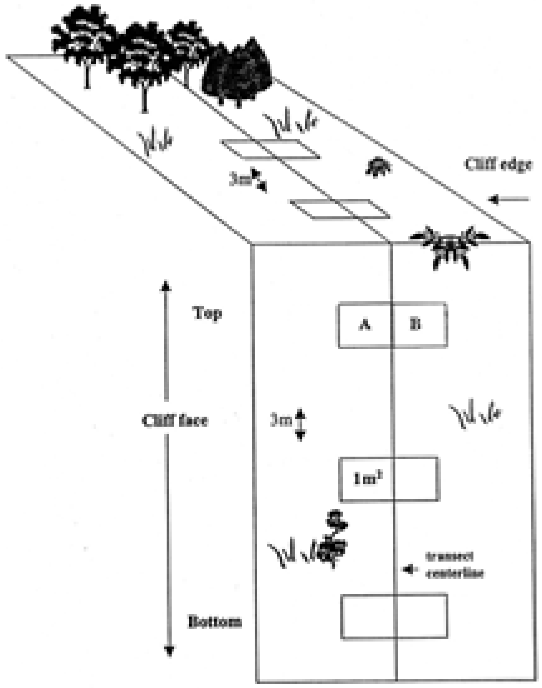

3m
Cliff edge
Top
A
B
Cliff face
3m
1m²
transect centerline
Bottom

Figure 7.

Figure 8.

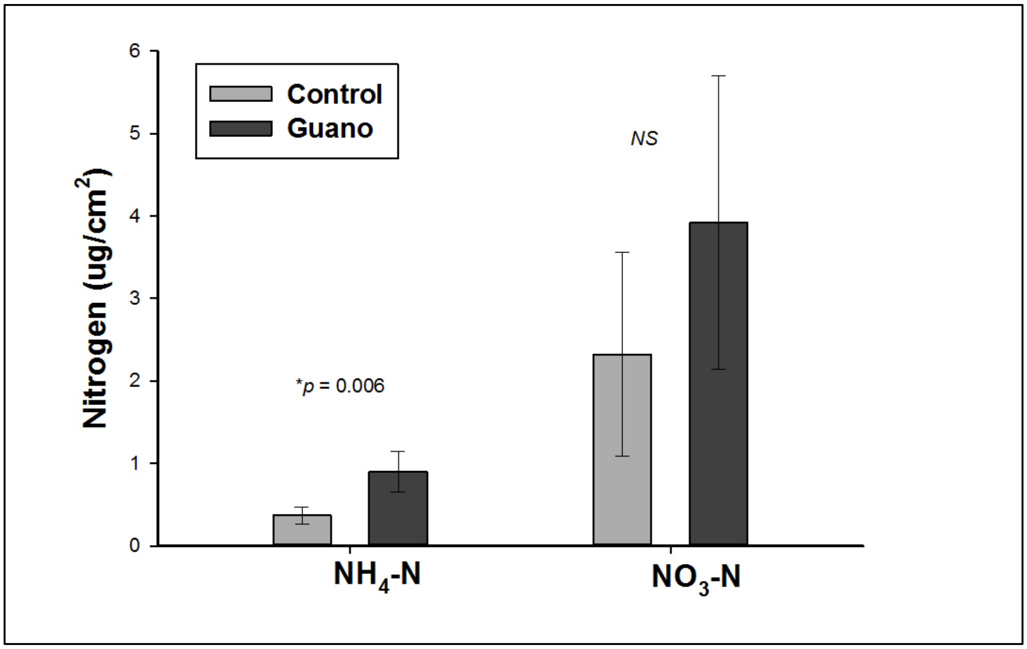


Figure 9.

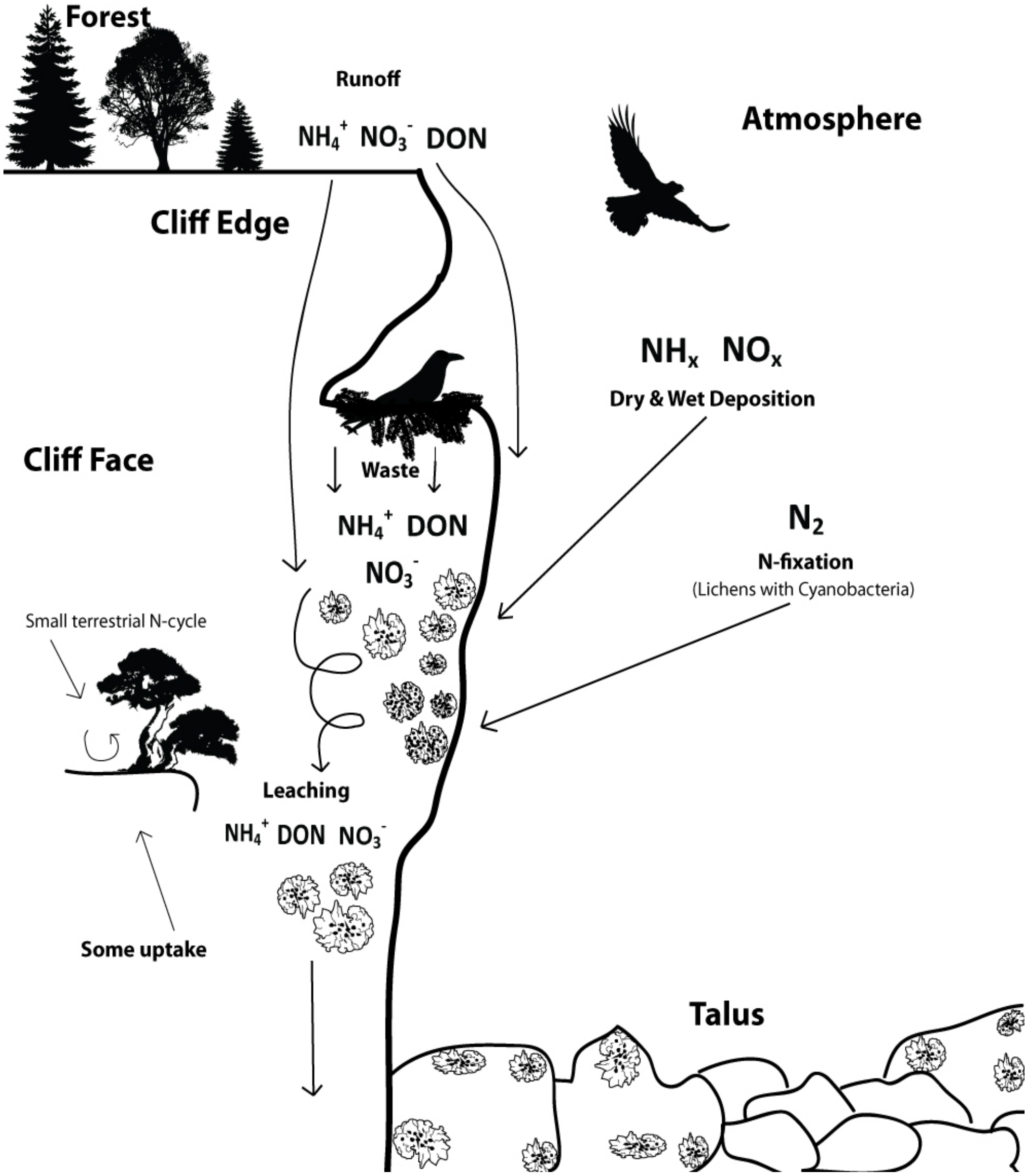

Forest
Runoff
NH_4^+ NO_3^- DON
Atmosphere
Cliff Edge
NH_x NO_x
Dry & Wet Deposition
Cliff Face
Waste
NH_4^+ DON
NO_3^-
N_2
N-fixation
(Lichens with Cyanobacteria)
Small terrestrial N-cycle
Leaching
NH_4^+ DON NO_3^-
Some uptake
Talus

Figure 10.

Figure 11.

Figure 12.

Appendix 1. Site Descriptions

Each study site is described, followed by descriptions of each transect. Site and species codes are listed. Species codes are as follows: Common raven (CORA), peregrine falcon (PEFA), and great horned owl (GHOW).

1. **Big Lost Cove Cliffs, Pisgah National Forest:** BLC 1, BLC 2. CORA

Big Lost Cove is located in Avery County, NC within the Pisgah National Forest at approximately 3,457 feet of elevation. Its remote cliffs remain largely untouched by climbers and hikers, although rock and ice climbing have occurred there during the past 20-30 years (Lesch-Huie 2014). Hunting parties and occasional backpackers have also made camps in the forest above the cliff line. The cliffs range from 70-200 feet tall and consist of rock from the Grandfather Mountain formation. Consequently, the cliffs largely face Northwest with views of Grandmother and Grandfather Mountain. The Grandfather Mountain formation is a cross-bedded Metagraywacke with local conglomerate, and often interlayered with metasiltstone and phyllite. Big lost Cove cliffs are varied in terms of slope and heterogeneity. In general, the cliffs are low-angle to vertical slabs with many seams that harbor large, deep mossy (*Selaginella rupestris*) hummocks. Lower angle cliffs give way to several large overhanging roof features, under which all four transects were located.

BLC1 Guano Transect (36.02406 N, 81.8417 W):

The common raven nest was located under a roof feature about 40 feet above the forest floor. Above the roof feature, the cliff rises to about 150 feet. Thus, the edge plot was not a true edge, but simply the area directly above the nest. The nest was located on a large ledge and was about 1 m wide with many sticks, debris, feathers and guano below the nest on the cliff face. The rock face is largely vertical, at an average of 85 degrees, with many horizontal seams, pockets and breaks. Lichens were the most abundant vegetational community type; including mostly crustose and tightly appressed lichens such as *Physcia subtilis*, *black and grey bubble crust*, and *white bubble crust*. Some mosses and vascular plants such as *Rhododendron catawbiense* and *Rhododendron maximum* were found growing in the talus.

BLC1 Control Transect (36.02408 N, 8184171 W):

This transect was very similar to the guano transect. It began on a ledge, encompassed a vertical face with high surface heterogeneity, and encountered a second ledge about 15 feet below the nest. The vegetational community was mostly lichen, but also contained some mosses and vascular plants, especially on ledges and in the talus. Abundant species included two crustose lichens, *black and grey bubble crust, white bubble crust,* the foliose *Lasallia papulosa,* and *Rhododendron catawbiense*.

BLC2 Guano Transect (36.02404 N, 081.4166 W):

The second site at Big Lost Cove Cliffs was a popular perch site, likely used by common ravens due to its relative proximity to the nest site. This site (BLC 2) was very similar to BLC 1, with a largely Northwest aspect and vertical slope. There was high surface heterogeneity on the rock face as well, with many seams, pockets and cracks. The BLC 2 guano and control transects were both located under a large overhang that was part of the same roof system that shaded the BLC 1 nest. Unfortunately, none of my traps would adhere to the cliff at the time of sampling. This may be due to the drastically colder temperatures exhibited on my sampling day, as this was the last transect we attempted to place traps on during the sampling season. The guano transect exhibited many ledges, with an excess of guano and some rodent poop observed as well in the cracks. Underneath the whitewash, we observed a thick band of eutrophic lichens *Physcia caesia* and *Caloplaca citrina.* Other common lichens on this transect included *Physcia subtilis, Parmotrema ultralucens,* and *Ramalina intermedia*. The bottom half of the transect consisted of many ledges collecting moisture and soil. The bottom half of the transect was dominated by vascular plant species such as *Kalmia latifolia*.

BLC2 Control Transect (36.02403 N, 081.84137 W):

The control transect was on a vertical, left-facing dihedral feature that experienced occasional runoff and algal growth. A ledge above the transect formed at the end of the roof system, likely providing the excess moisture. About 15 feet above the talus, the rock face became a low-angle slab. Some vascular species and mosses occurred on this transect, but commonly observed species were the lichens *Melanellia culbersonii, Lepraria neglecta* and *tan crust*.

2. Buzzard’s Roost, Pisgah National Forest: BUZ. PEFA

Buzzard’s Roost is an approximately 250 foot tall cliff located at 2,400 feet of elevation in Haywood County, NC. The cliff itself is about 400 feet above the Pigeon River and Interstate 40 in the Pisgah National Forest. Although named “Buzzard’s Roost” this site is actually a peregrine falcon nesting area monitored by the NCWRC and closed each year to climbing, although no recent climbing activity has occurred here. The eyrie is located about 20 feet below the top of the cliff. The rock type is Longarm Quartzite, a cross-bedded, feldspar rich metamorphic rock formed in the late Proterozoic era. This rock type can also contain local areas of conglomerate slate or metasillstone. Most of the cliff line is broken up into a series of arêtes and dihedrals. The main scenic overlook is a prominent prow formation. The edge plot areas of both transects were highly impacted areas, especially on the control transect. The top of the cliff is a popular scenic overlook that is close to an unimproved road.

BUZ Guano Transect (36.45804 N, 081.33344 W):

Primarily Northeast facing, the guano transect was a steep vertical face (average slope of 80 degrees) and dihedral, broken up by horizontal ledges and deep crack systems. Inside one of the deep cracks was the peregrine nest site. A large amount of whitewash, feathers, and prey remains are visible around and below the nest ledge. Popular perch sites below and above the nest itself also existed on this transect. Below the nest ledge was a vertical face that eventually met a large overhanging area that made it difficult to sample. To the right of the nest ledge, was a large overhanging roof feature. The dominant vegetation type was lichen, with some vascular plants (*Rhododendron maximum*, *Tsuga Canadensis*) and moss (*Bazzania trilobata*) on the edge plots. Abundant lichen species included *light grey verrucose crust*, *white-grey crust*, *Chrisothrix* sp., *Cladonia* sp., *Punctelia subreducta*, *Lasallia papulosa*, *Rhizocarpon* sp., and *Physcia subtilis*.

BUZ Control Transect (36.45804 N, 081.33344 W):

The control was located 15.4 feet from the nest transect because we could not find another suitable sampling location due to the large prow feature to the east. The transect was also a steep vertical face with Northeast aspect, and a similar average slope to the guano transect: 70 degrees. It contained many ledges at the top, with multiple trees growing out of a large amount of soil collected on the ledges. The vertical rock face eventually lead to an intensely steep roof, making it extremely difficult to sample. Some occasional peregrine falcon feathers were seen on the transect, probably due to occasional perch use of the ledges by the birds using the nearby eyrie. *Vaccinium stamineum*, *Betula lenta* and *Polypodium virginianum* were the main vascular plant species living on the transect. Mosses comprised a small percentage of the vegetational community, where as lichens largely populated the cliff. Foliose lichens *Myelochroa aurulenta*, *Parmotrema melissii*, and *Umbillicaria mammulata* proliferated the transect, along with crustose *Rhizocarpon* sp. and fruticose *Usnea amblyoclada*.

3. Chimney Rock State Park. CHM. PEFA

Chminey Rock State Park is a 1,000 acre park located in Rutherford County, NC about 25 miles Southeast of Asheville, NC in the Hickory Nut Gorge. The Broad River flows through the gorge and borders the park on its North side. The park is located above the town of Chimney Rock, NC (a popular tourist destination). The transects were located at approximately 2,080 feet of elevation on a 315-foot tall metamorphic monolith that is the main attraction of the park. The rock type is Cambrian garnet-mica schist interlayered with amphibolite. Peregrine falcons have historically nested at en eyrie about 150 feet below the top of the cliff in the main horizontal crack system.

CHM Guano Transect (35.255904 N, 082.15530 W)

The guano transect was located approximately 100 feet below the top of the cliff at a prominent perch site. Due to the extreme nature of the rappels to the sample site, the high impact of a tourist trail at the top of the cliff, and the location of the site 100-150 feet below the top of the cliff, Edge plots for the transect were located on the face of the cliff, but above the nest site. We could not safely access the actual nesting site of the peregrine falcons due to the nature of the site. The prominent roost site exhibited a clear visual lichen community change underneath the guano deposit.

The transect was primarily North facing, with an average slope of 84 degrees and generally low surface heterogeneity. Lichens were the only vegetational community present, dominated by umbillicate foliose lichens *Lasallia papulosa*, *Lasallia pennsylvanica*, in all parts of the transect and squamulose *Cladonia caespitica* in a large swath underneath the whitewashed area.

CHM Control Transect (35.255948 N, 082.151033 W):

The control transect was located approximately 65 ft West of the guano transect. It was also primarily North/Northwest facing, with an average slope of 89 degrees, and generally low surface heterogeneity. The transect was located about 50 feet below the top of the cliff, and in a slightly seepy area. The excess moisture may have caused most of the ion traps to fall off below plot 2. Moss (mostly *Selaginella rupestris*) was found growing only on the edge plot of this transect; lichens were the only other vegetational community. Again, *Lasallia pennsylvanica* was abundant along with tightly-appressed foliose lichen *Physcia subtilis* and crustose *Rhizocarpon sp.*

4. Goat Rock. GOA. Vilas, North Carolina. CORA?

Goat Rock is a small cliff (about 45 feet tall) located on private property in western Watauga County, NC. It is largely untouched by any user group, barring occasional bouldering by the land owner. A large nest, likely a common raven was located about 20 feet off the ground. The nest site had been used during the 2014 season, as was evidenced by fresh guano, debris and nesting material, but a confirmed species sighting was not made. There are no clear trails to the site itself, and access is difficult. The cliff itself is broken up by ledges, cracks and a large roof that shades the guano transect and part of the control. The slope of the forest above was very steep, and ended at the top of my transects. Thus, the edge transects contain soil and leaf litter. Geologically, the cliff is well-foliated biotite granitic gneiss.

GOA Guano Transect (36.29108 N, 81.78748 W):

The nest was located on a ledge underneath a vertical face and a large overhanging roof. Underneath the nest, the cliff turned into a steep roof again. The guano transect had a lack of vegetation, largely harboring species of *Lepraria* probably due to its location under a series of overhanging roofs. A great amount of debris, sticks, guano and feathers was observed in the talus directly under the nest.

GOA Control Transect (36.29105 N, 081.78744 W):

The control transect was very similar to the guano transect, but not completely capped by a roof. The lower section was shaded by the overhang, but the upper section angled out of the roof and ended as a vertical face. A series of horizontal cracks cut through the cliff face along with a few small ledges. Green algae, *Lepraria* sp. and a few mosses including *Eurynchium ripariodes* were common on this transect.

5. New River State Park: NRS. CORA

The New River State Park nest site was reported to us by park rangers and an enthusiastic group of bird watchers belonging to the High Country Audubon Society (HCAS). It was an unusual site that was located on a very short band of broken cliff line across the New River from the main section of the park. There were no trails and no bridges to the site. The location given to us was only approximate, since the birds could only be observed from across the river. Citizen scientists reported the ravens entering a dense stand of hemlock trees with nesting material and food. Sampling at this site necessitated access by canoe. The broken cliff band was only about 25 feet tall at the nest site, and the nest itself was only about 15 feet above the talus. The choice of control transect location was difficult due to the limited availability of adjacent cliff line. The remainder of the cliff was either severely overhung, too short to sample, or consisting of dangerously loose rock. The transects faced West/Northwest at 2,600 ft of elevation with a highly variable slope and consistently high surface heterogeneity. The rock itself was dark grey mafic amphibolite; it was well foliated and occasionally very loose, thus researchers were careful when sampling the area.

NRS Guano Transect (36.45817 N, 81.33304 W):

The nest was located in a blocky, obtuse dihedral formation with sharp edges. Primarily low angle, although becoming vertical for the last 10 feet. The nest was a 3ft wide stick nest in the right side of the dihedral on a small ledge. The guano was seeping down the side of the dihedral, although the left side was fairly clean of whitewash. The nest itself consisted of large sticks and pine needles as lining. Much debris covered the talus area and some of the cliff; shredded plastic, animal hair, feathers and other remains. The vegetation on this transect consisted of a mix of lichens- *Phaeophyscia rubropulcha*, *Lepraria* spp., *Pertusaria* spp.; mosses dominated by *Bryum c.f. caespiticum*; and vascular plants – *Huechera villosa*, *Phytolacca americana*, *Carex laxiflora* and *Solidago curtissi*.

NRS Control Transect (36.45827 N, 81.33292 W):

The control transect was similar to the guano transect in aspect, slope and surface heterogeneity except it contained more moisture. It was difficult for us to adhere the traps to much of the left side of the control transect due to the moisture there. Much of the vegetation was dominated by *Lepraria* spp., *Pertusaria* spp., *Huechera villosa* and mosses such as *Bryum c.f. caespiticum*.

6. Pilot Mountain State Park: PIL. CORA

Pilot Mountain State Park protects an iconic quartzite monadnock and cliff line that have been popular with Piedmont residents in North Carolina since 1968. The park is located in Surry County, NC just north of Greensboro and sees a high volume of hikers, motor tourists and rock climbing groups. The transects were located in a high-traffic climbing area where a raven pair has attempted to nest for the last 2 years. Other perch areas were noted around the park, and potential nests were reported to us on the large pinnacle, however none were located after a thorough search. This area is known as a raven nesting area, and could potentially harbor more nests – a thorough nest search of this area is suggested for future studies. The nest was large 1-2 m wide, consisting of large sticks. Guano was evident on the nest transect. The cliff line, situated at 2,421 feet of elevation faced West/Northwest with a vertical slope and medium-high surface heterogeneity.

PIL Guano Transect (36.34156 N, 80.48754 W):

On the high-traffic guano transect, all of my ion traps remained intact. This is likely because rock climbers were aware of the nest and closures to the area during nesting season, and may have avoided removing the traps. To the left of the climbing route, about 5 feet deep in a large chimney-like crevice, the ravens had built their nest. The nest area itself was slightly seepy and mossy. To the right of the nest on the climbing route, the rock was dry and largely devoid of vegetation due to high climbing activity. The dominant species living near the nest were the lichens *Physcia subtilis*, *Parmelinopsis minarum*, *Lepraria* spp., and *Chrisothrix* sp.

PIL Control Transect (36.3416 N, 08048756 W):

The control transect was largely similar to the guano transect in structure except that it lacked the large crack/chimney feature where the nest was contained. It did have cracks, ledges and was also a highly-trafficked climbing route. The main vegetational species on this transect were also lichens: *Buellia* sp., *Dimelaena* sp., *Lepraria* sp., and *grey rimose crust*. Unfortunately, we returned after two months to find that all of the ion traps had been removed from this transect. We suspect that rock climbers may have removed them.

7. Table Rock. TAB. Pisgah National Forest: GHOW?

Table Rock is a freestanding mountain that shares the Grandfather Mountain formation metagraywacke with the Big Lost Cove Cliffs. It is a popular traditional climbing destination but it is not as highly impacted or disturbed as Pilot Mountain's cliffs due to the nature of traditional climbing. Table Rock, at 4,101 feet of elevation is my second highest study site. It is located on the east rim of the Linville Gorge, on the edge of the Linville gorge wilderness area. The site was reported to us by a member of the SACC at Appalachian State who found the nest after breeding season had ended. We thus could not identify the species or confirm that it was used as a nesting site specifically. However it had been recently used at least as a popular roost, and likely had been a nest site abandoned for the season. The birds had left a significant amount of guano and debris to potentially impact the cliff. The cliff had an aspect and an average slope of with high surface heterogeneity (many pockets, cracks and ledges), with many large mossy hummocks consisting of many lichen and moss species but mainly *Selaginella rupestris* and *Cladina rangeferina*.

TAB Guano Transect (35.532580 N, 081.525656 W)

The nest or roost site was located in a deep crack feature at about 130 feet tall on the cliff face. A popular climbing route "White Lightning" uses the crack system as a place for natural gear, however many climbers reported to us that they had been avoiding the direct finish to "White Lighting", finishing instead to the right on a route called "The North Ridge" due to the unpleasant nature of climbing though the heavy guano deposit. Some of my ion traps disappeared and may have been removed by climbers, but we did retain some of the traps that were placed near the nest. Vegetation was diverse on both transects, consisting of a mix of moss, lichen and vascular plant species. The hummocks harbored much diversity in lichens and mosses, but many crustose species dominated the percent cover estimates as well. The vascular plants *Hydatica petiolaris*, *Rhododendron catawbiense* and lichen *Lasallia papulosa* were common on this transect.

TAB Control Transect (35.532287 N, 081.525709 W)

The control transect was largely similar in structure and vegetation, containing a large horizontal crevice instead of a vertical one. Surface heterogeneity, however, largely remained high and the slope was also similar. The control area is also occasionally climbed as part of a more advanced extension to “White Lightning”.

8. Snake Mountain (Elk Knob State Park) SNA. CORA:

Snake Mountain is a 5,518 foot peak within Elk Knob State Park, west of Elk Knob itself. The transects were located at approximately 5,300 feet of elevation and were my highest transects in the study. Doug Blackford and Martha Cutler of the HCAS reported the common raven nest at Snake Mountain. They enthusiastically monitored the site through the fledging of the young ravens. The Snake Mountain site consists of an exposed 60-80 foot tall cliff line about 200 feet below the summit. There are no trees above the site, although the talus area was shaded by deciduous forest and had a rich diversity of vascular plants. The cliff consists of the same mafic amphibolite of the New River State Park site, however the rock was much more solid. Some ice and rock climbing has taken place at the study cliffs in the past 20 years, but was limited to a small group of local individuals (Willis 2014). A piton was found on the control transect, and was reported to have been placed there in the last two years by local climbers (Willis 2014). The cliffs largely had high surface heterogeneity, (many cracks, pockets and seams) a North aspect and an average slope of 80 degrees.

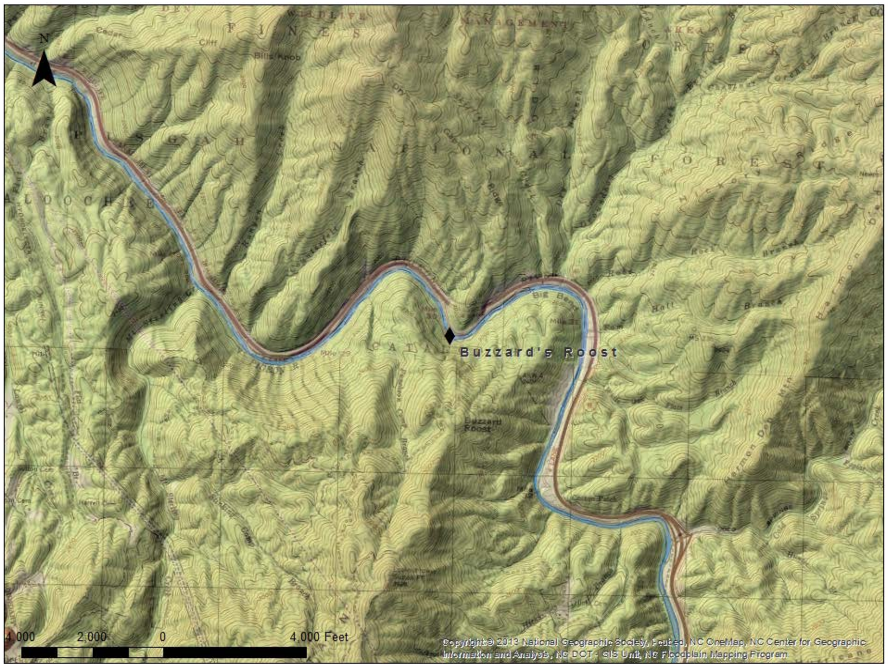
SNA Guano Transect (36.34216 N, 081.70393 W):

This nest transect had more moisture than the control but similar surface heterogeneity and slope. There was a high percentage cover of moss species, with moss hummocks in some areas. A large swath of the eutrophic lichen *Xanthoria candelaria* was found growing directly under the common raven nest. The nest itself was about 3ft deep, 2ft high and filled with silt, small feathers, debris and many sticks. Whitewash was evident on the cliff underneath the nest and at perch sites on the transect.

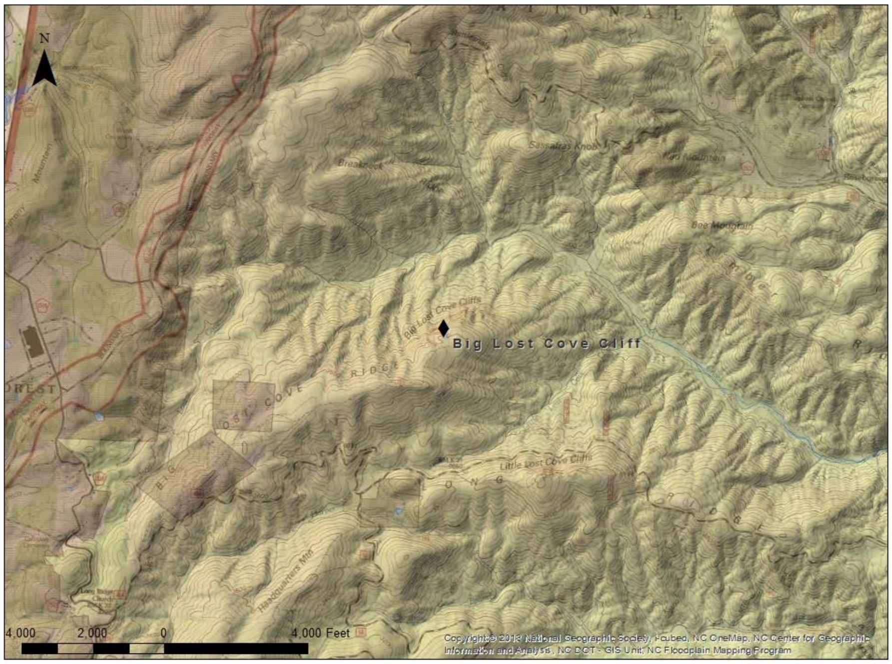
SNA Control Transect (36.34217 N, 081.70412 W):

The control transect consisted of many ledges, with an approximately 18 inch wide vertical crack system where the piton was found. This transect trended into a small dihedral where it became low-angle. Surface heterogeneity was higher towards the base of the cliff. Common species on this transect included crustose lichens *Fuscidea* sp., *Lecidea* sp., *Buellia* sp., *Ochrelochia* sp., foliose lichen *Myelochora obsessa*, vascular plants *Hydatica petiolaris*, *Woodsia* sp., and a diverse community of mosses; *Dicranella heteromala*, *Bazzania trilobata*, *Bryhnia graminicolor*.

Appendix 2. Maps Of Study Sites



Buzzard's Roost study site, Pisgah National Forest, NC.



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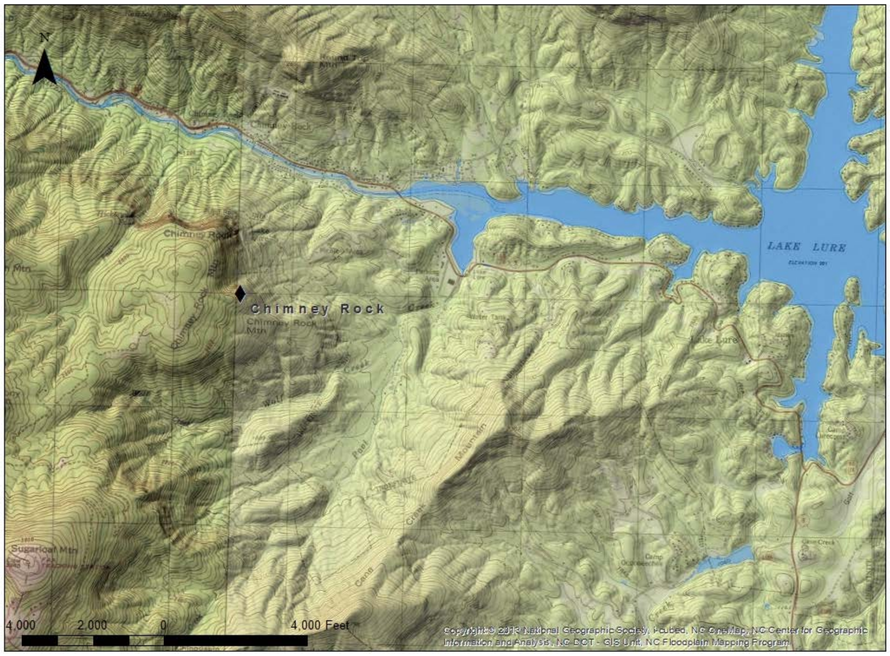
Big Lost Cove Cliffs study site, Pisgah National Forest, NC.



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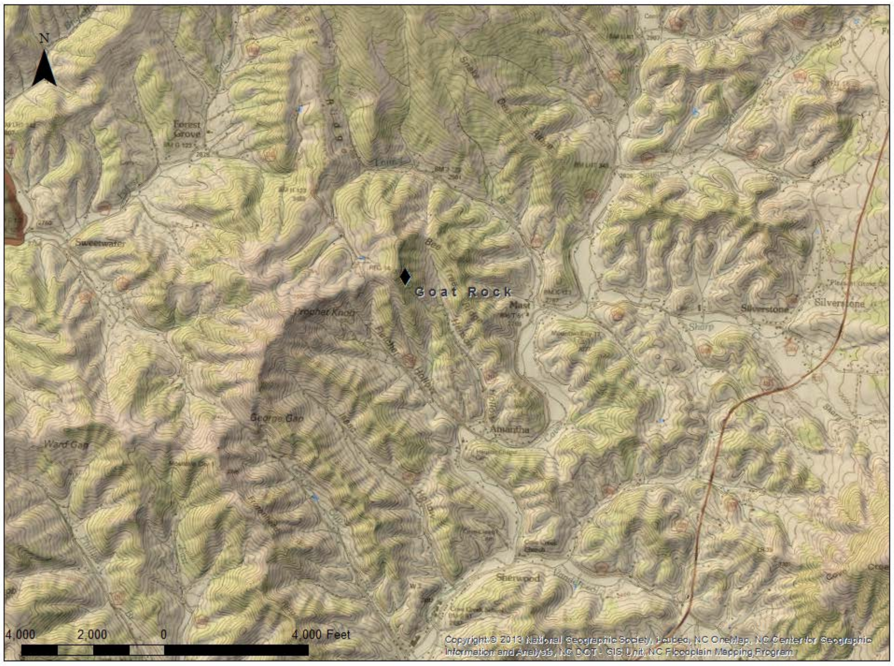
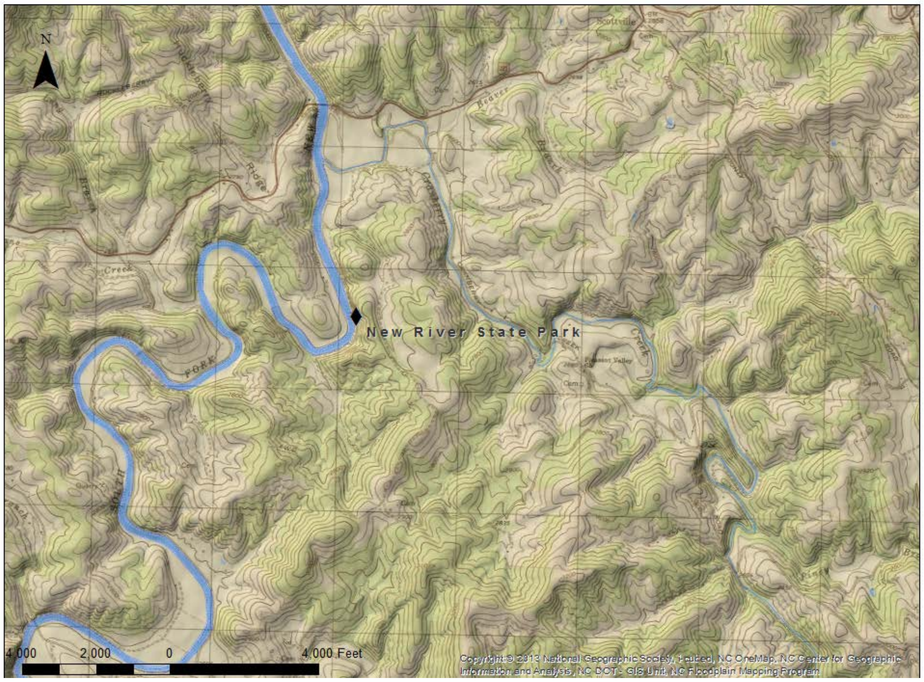
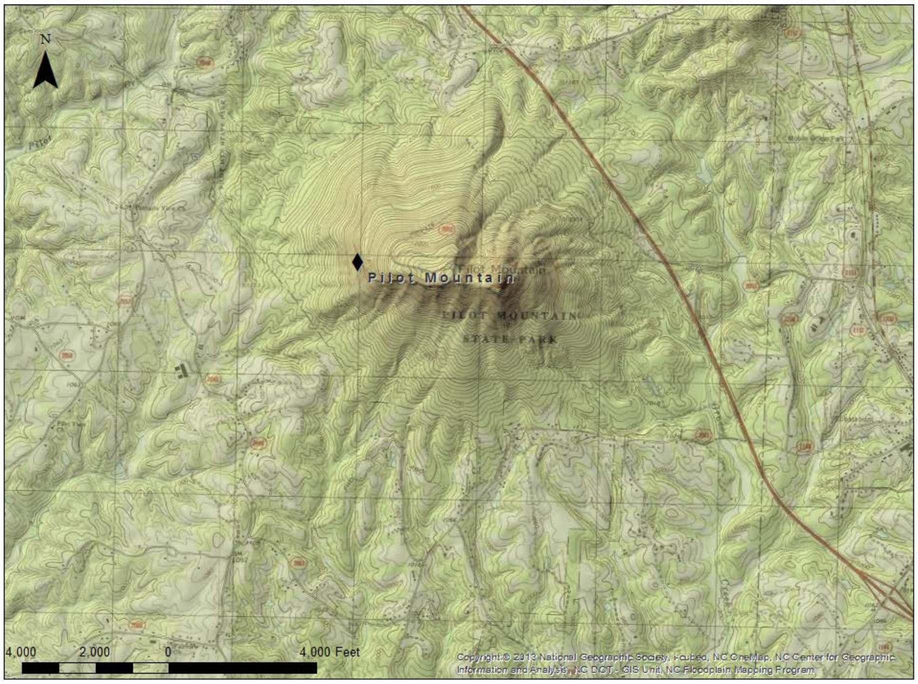
Chimney Rock study site, Chimney Rock State Park, NC.



Goat Rock study site near Sugar Grove, NC.



New River study site, New River State Park, NC.



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Pilot Mountain study site, Pilot Mountain State Park, NC.

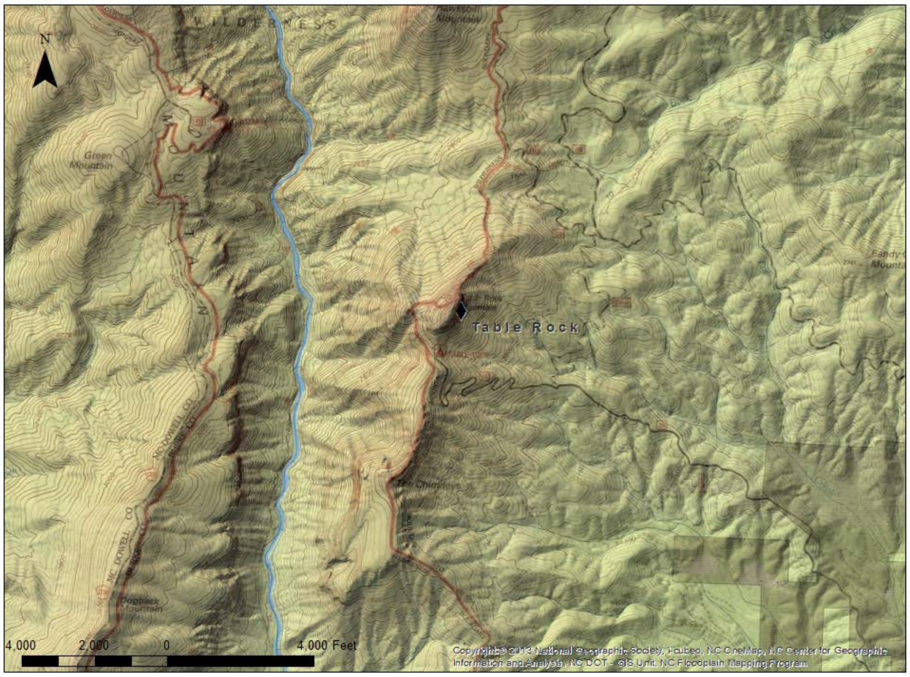

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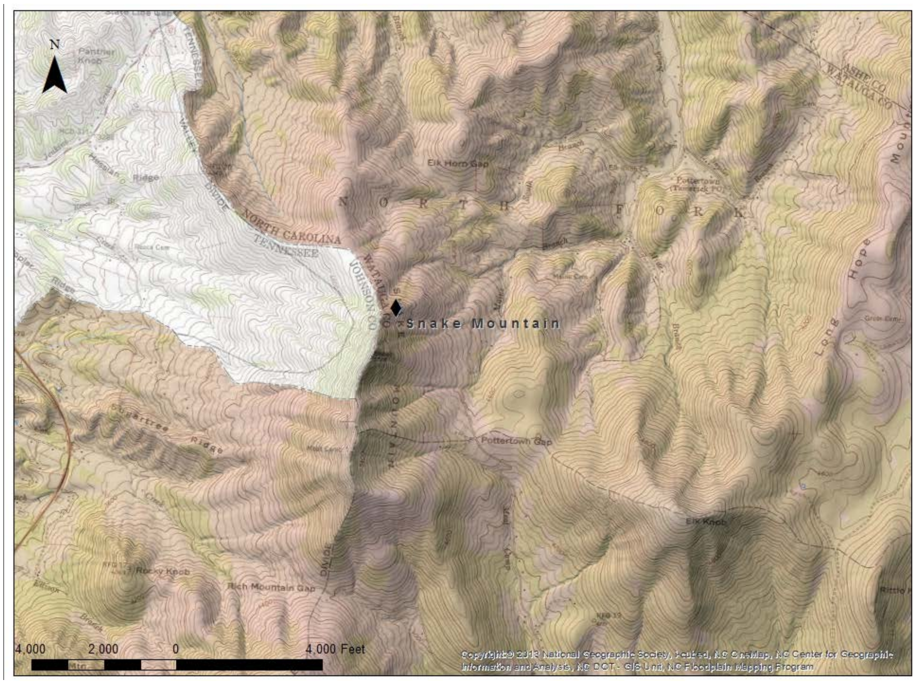
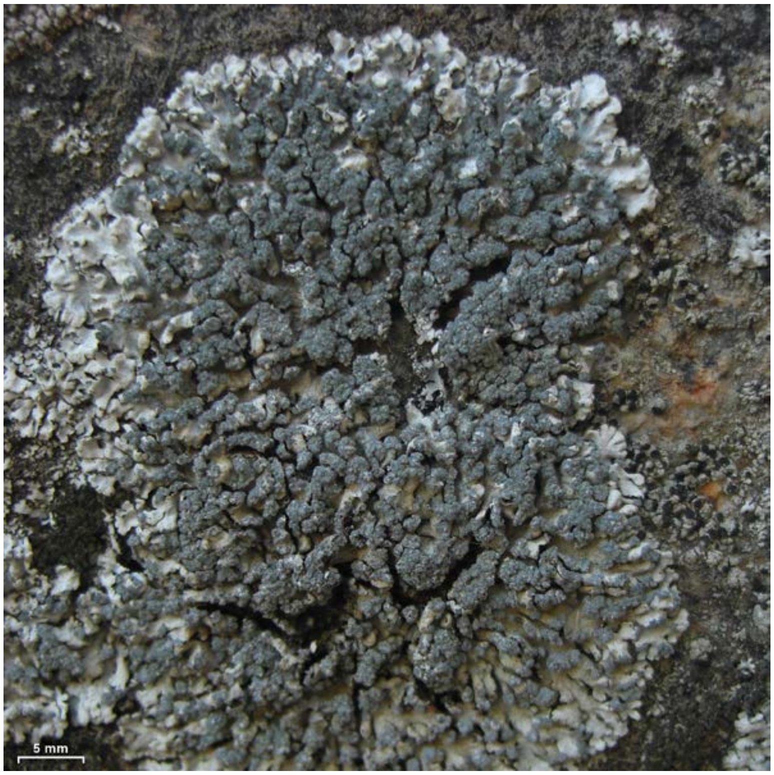
Table Rock study site, Pisgah National Forest, NC.



Snake Mountain study site, Elk Knob State Park, NC.

Appendix 3. Eutrophic Lichen Species Found in Study

Eutrophic orange lichen *Xanthoria candelaria*. Many orange lichens in the genus *Xanthoria* are eutrophic, and typically observed near areas enriched by animal excrement. (Jason Hollinger, 2014)



A lichen commonly found near bird perches, *Physcia caesia* is a eutrophic species that typically grows on rock substrates. (Jason Hollinger, 2014).

Appendix 4. Lichen Species List

Lichen samples were identified to species or genus with a morphotype descriptor when possible. If resources did not allow for the identification of species or genus, samples were classified by morphotype only.

black and grey bubble crustose	
black and grey crustose	
black crustose	
black crustose 2	
black dot crustose	
blue-gray sorediate crustose	
Bryoria furcellata	(Fr.) Brodo & D. Hawksw.
Bryoria sp.	Brodo & D. Hawskw
Buellia sp. black hypothallus	
Buellia sp. dark grey	
Buellia sp. grey	
Caloplaca citrina	(Hoffm.) Th. Fr.
Canoparmelia alabamensis	(Hale & McCull) Elix.
Chrisothrix sp.	Mont.
Chrisothrix sp. yolk yellow	
Cladina rangiferina	(L.) Nyl.
Cladonia caespitica	(Pers.) Flörke
Cladonia furcata	(Huds.) Schrad.
Cladonia pleurota	Flörke

Cladonia sp. P. Browne	
Cladonia sp. green	
Cladonia sp. grey	
Cladonia sp. mint 1	
Cladonia sp. mint 2	
Cladonia sp. pixie cup	
Cladonia sp. white	
Cladonia strepsilis	(Ach.) Grognot
cream patch crustose	
Dimelaena sp. Norman	
Fuscidea sp.	V. Wirth & Vèzda
green areolate crustose	
green black crustose	
green crustose	
grey black hypothallus	
grey circular crustose	
grey patch crustose	
grey rimose crustose	
grey verrucose crustose	
grey wart crustose	
Hypocenomyce scalaris	(Ach. ex Lilj.) M. Choisy
Hypotrachyna revoluta	(Flörke) Hale
Imshaugia aleurites	(Ach.) S.F. Meyer
Lasallia papulosa	(Ach.)Llano
Lasallia pennsylvanica	(Hoffm.) Llano
Lecanora sp. grey	
Lecanora sp. tan	
Lecidea sp.	
Lecidea sp. brown	

Lepraria incana	(L.) Ach.
Lepraria lobificans	Nyl.
Lepraria neglecta	(Nyl.) Erichsen
Lepraria sp. blue	
Lepraria sp. bright yellow	
Lepraria sp. brown	
Lepraria sp. green	
Lepraria sp. light grey	
Lepraria sp. light mint	
Lepraria sp. mint	
Lepraria sp. neon green	
Lepraria sp. peach	
Lepraria sp. yellow green	
Lepraria sp. yellow mint	
Leptogium cyanescens	(Rabenh.) Körber
light grey verrucose crustose	
Melanelia culbersonii	(Hale) Thell
Melanelia sp.	Essl.
mint areolate crustose	
mint crustose	
mint crustose lobed	
mint foliose-crustose	
Myelochroa aurulenta	(Tuck.) Elix & Hale
Myelochroa obsessa	(Ach.) Elix & Hale
Ochrolechia sp.	A. Massal.
Parmelia omphalodes	(L.) Ach.
Parmelia saxatilis	(L.) Ach.
Parmelia sp.	Ach.
Parmelinopsis minarum	(Vainio) Elix & Hale

Parmelinospis horrescens	(Taylor) Elix & Hale
Parmotrema crinitum	(Ach.) M. Choisy
Parmotrema melissii	(C.W. Dodge) Hale
Parmotrema ultralucens	(Krog) Hale
Pertusaria sp. white	
Phaeophyscia rubropulcha	(Degel.) Essl.
Physcia caesia	(Hoffm.) Fürnr.
Physcia sp.	(Schreber) Michaux
Physcia subtilis	Degel.
Punctelia subreducta	(Nyl.) Krog
Ramalina intermedia	(Delise ex. Nyl.) Nyl.
Ramalina pollinaria	(Westr.) Ach.
red hypothalline crustose	
Rhizocarpon sp.	Ramond Ex Dc.
rust crustose	
spotted grey crustose	
Stereocaulon dactylophyllum	Flörke
tan crustose	
tan patch crustose	
Umbillicaria mammulata	(Ach.) Tuck
Usnea amblyoclada	(Müll. Arg.) Zahlb.
Usnea sp.	Dill. Ex Adans.
white areolate	
white bubble crustose	
white crustose	
white crustose small	
white rimose crustose	
white-grey crustose	
Xanthoria candelaria	(L.) Th. Fr.

Appendix 5: Vascular Species List

Acer rubrum	L.
Adiantum sp.	L.
Ageratina altissima var roanensis	(Small) Clewell & Woot.
Amelanchier sp.	Medik.
Arisaema triphyllum	(L.) Schott *
Aristolochia sp.	L.
Asplenium montanum	Willd.
Asplenium trichomanes	L.
Betula lenta var. lenta	L.
Carex laxiflora	Lam.
Carex pensylvanica	Lam.
Carex sp.	L.
Cornus alternifolia	L. f.
Dryopteris marginalis	(L.) A. Gray
Eurybia divaricata	(L.) G.L. Nesom
Galax urceolata	(Poir.) Brummit
Heuchera villosa	Michx.
Hydrangea arborescens	L.
Kalmia latifolia	L.
Laportea canadensis	(L.) Weddell
Oxydendrum arboreum	(L.) DC.
Paronychia argyrocoma	(Michx.) Nutt. **
Parthenocissus quinquefolium	(L.) Planch.

Phytolacca americana	L.
Poaceae sp.	
Polypodium virginianum (complex)	L.
Rhododendron calendulaceum	(Michx.) Torr.
Rhododendron catawbiense	Michx.
Rhododendron maximum	L.
Rubus sp.	L.
Saxifraga michauxii	Britton
Selaginella rupestris	(L.) Spring
Smilax sp.	L.
Solidago curtisii	Torr. & A. Gray
Sorbus americana	Marshall
Symphyotrichum prenanthoides	(Muhl. Ex Willd.) G. L. Nesom
Tsuga canadensis	(L.) Carrière
Unknown vascular 1	
Unknown vascular 2	
Urtica sp.	L.
Vaccinium erythrocarpum	Michx.
Vaccinium sp.	L.
Vaccinium stamineum	L.
Viola sp.	L.
Woodsia sp.	R. Br.

** Wetland species*

*** Threatened in Tennessee*

Appendix 6: Bryophyte Species List

Liverwort Species

Kurzia sylvatica	(Evans) Grolle
Diplophyllum apiculatum	(Evans) Steph.
Harpalejeunea ovata	(Hook.) Schiffn.
Metzgeria furcata	(L.) Dum.
Scapania nemorea	(L.) Grolle
Porella platyphylla	(L.) Pfeiff.
Bazzania trilobata	(L.) S. Gray
Lejeunea ulicina	(Tayl.) Gott.

Moss Species

Leucobryum albidum	(Brid. ex P. Beauv.) Lindb.
Atrichum angustatum	(Brid.) Bruch & Schimp. in B.S.G.
Bryhnia graminicolor	(Brid.) Grout
Pseudotaxiphyllum elegans	(Brid.) Iwats.
Plagiomnium ciliare	(C. Müll.) T. Kop.
Leucobryum glaucum	(Hedw.) Ångstr. in Fries
Leucobryum cf. glaucum	(Hedw.) Ångstr. in Fries
cf. Ceratodon purpureus	(Hedw.) Brid.
Atrichum undulatum (s.l.)	(Hedw.) P. Beauv.
Eurynchium riparioides	(Hedw.) Rich
Dicranella cf. *heteromala*	(Hedw.) Schimp.

Dicranella heteromala	(Hedw.) Schimp.
Thuidium delicatulum	(Hedw.) Schimp. *in* B.S.G.
Leptobryum pyriforme	(Hedw.) Wils.
Sematophyllum cf. *demissum*	(Wils.) Mitt.
Polytrichum pallidisetum	Funck
Dicranum montanum	Hedw.
Bryum cf. *caespiticium*	Hedw.
Hypnum imponens	Hedw.
Dicranum scoparium	Hedw.
Campylopus tallulensis	Sull. & Lesq.
Dicranum cf. fuscesens	Turn.
Dicranum fuscescens	Turn.
cf. Dicranella sp.	
Bryum sp. 1	
Bryum sp. 2	
cf. Pohlia sp.	
Unknown Moss club moss	
Unknown Moss 1	
Unknown Moss 2	
Unknown Moss 3	
Unknown Moss 4	
Unknown Moss 5	

Appendix 7: Legends For Geologic Map Of Study Area

Vita

Angela Langevin graduated from the forested domain of Sewanee with her B.S. in Ecology and Biodiversity. A lifelong bird enthusiast, she originally aimed to study avian conservation biology. However, inspired by her love for rock climbing and experiences with fascinating cliff-dwelling organisms in Yosemite and Chattanoooga, she chose to come to the cliff ecology research lab at Appalachian State University. She hopes to use her Master's degree to teach the next generation of young minds, and to infuse them with scientific literacy. Her experiences with cliff ecology are invaluable to the rock climbing community and she will strive to use her knowledge to help the climbing community continue an important dialogue with biologists and land managers. Lastly, Angela hopes to continue having great adventures and exploring the earth's wild places.