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Description of Rich Montane Seeps and Effects of Wild Pigs on the Plant and Salamander Assemblages

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ABSTRACT.—Rich Montane Seeps are rare wetland communities endemic to high elevations of the southern Appalachian Mountains. Comprehensive data on the flora and fauna associated with these communities are lacking. Recent surveys indicate the rooting by nonnative wild pigs (*Sus scrofa*) may be affecting these communities. This study describes the abiotic and biotic features of Rich Montane Seeps across the Great Smoky Mountains National Park (GSMNP), investigates the effects of wild pigs on plant and salamander communities, and examines habitat attributes that influence pig disturbance. In our study a Rich Montane Seep was defined as any wetland with sheet flow occurring in hardwood forests above 1067 m. Pig disturbance and habitat attributes were measured in 1-m^2 plots placed at 5 m intervals along a transect located on the longest axis of each seep. Habitat attributes measured included plant cover, plant richness, surface water, substrate, down woody debris, and shrub and tree densities (sampled in 3 m diameter circular plots). Salamanders were also sampled in each 1-m^2 plot, identified to species when possible, and classified as larva, juvenile or adult. Thirty-five seeps, representing 24 drainages, were sampled. Rich Montane Seeps were characterized as small, linear wetlands with an open canopy, dense herbaceous vegetation, and few trees or shrubs. One hundred eighty species of plants (132 herbs, 35 shrubs, and 13 trees) and 10 species of salamanders (97 adults, 204 juveniles, 14 larvae) occurred in seeps, including eight plant species and three salamander species of conservation concern. Forty-nine percent of seeps and 54% of drainages had evidence of pig disturbance. Disturbance within seeps varied from 0-96% (mean = 21%). Wild pigs negatively affected plant cover and plant richness. Wild pigs also had a negative effect on salamander surface density, but to a lesser extent than on plants. Amount of pig disturbance was negatively associated with slope. These results strongly suggest wild pigs are threatening the ecological integrity of Rich Montane Seeps across their range by negatively affecting the plant and salamander communities, particularly in seeps occurring on flat terrain.

INTRODUCTION

High Elevation Seeps are rare wetland communities endemic to the southern Appalachian Mountains (NatureServe, 2013). Two types are currently recognized and differentiated by the presence of *Sphagnum*: High Elevation Boggy Seep, which includes

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Sphagnum and generally occurs in Spruce (*Picea*) - Fir (*Abies*) Forests; and Rich Montane Seep, which lacks *Sphagnum* and generally occurs in Northern Hardwood Forests (Schafale, 2012; NatureServe, 2013). Both are of high conservation concern. High Elevation Boggy Seeps are globally ranked G2 (imperiled), and Rich Montane Seeps are globally ranked G3 (vulnerable; NatureServe, 2013). These small isolated wetlands are scattered throughout the mountains, with their distribution related to the strike and dip of metamorphic foliation and fractures in the rock that occur at high elevations (Schafale and Weakley, 1990). However, because of their remoteness and small size, only limited information is available on their biotic and abiotic attributes. For example only five sites were sampled to describe the vegetation composition of Rich Montane Seeps for the entire state of Virginia (Virginia Natural Heritage Program, 2012) and only four sites were sampled to describe the vegetation of Rich Montane Seeps in the Great Smoky Mountains National Park (White *et al.*, 2003).

High Elevation Seeps are important because they often are the original discharge source of groundwater for headwater streams (Gomi *et al.*, 2002; Nadeau and Rains, 2007). As a result they help maintain natural base flow regimes, regulate sediment export and nutrient retention, and contribute to the chemical signature of stream systems (Gomi *et al.*, 2002; Nadeau and Rains, 2007). Their unique soil and hydrologic features allow High Elevation Seeps to provide habitat for many rare and endemic plants and distinct floral communities (Schafale and Weakely, 1990; White *et al.*, 2003; Jenkins, 2007). High Elevation Seeps also are important to wildlife, particularly salamanders (Petranka, 1998; Grover and Wilbur, 2002). Because of their nearly constant flows, High Elevation Seeps provide critical breeding habitats (Petranka, 1998) and serve as refugia for stream-breeding salamanders found at high elevations (Grover and Wilbur, 2002).

Threats to these rare communities are generally undocumented. However, they are thought to have a low tolerance to disturbance, especially atmospheric and terrestrial perturbations (Lowe and Likens, 2005). Schwartzman (2008) and Rossell (2013) recently reported wild pigs (*Sus scrofa*) are a potential threat to the plant and salamander communities in Rich Montane Seeps in North Carolina. However, the pervasiveness of pig disturbance in these rare communities is unknown.

Wild pigs are an exotic species that can have devastating effects on plant and animal communities (Mayer, 2009a; Barrios-Garcia and Ballari, 2012). The majority of their disturbance is related to rooting for food (Mayer, 2009a). Wild pigs are opportunistic omnivores that can disturb large areas while searching for below-ground plant materials (*e.g.*, hard mast, roots, tubers, corms), and animals that inhabit the soil and litter layers, including salamanders (Bratton, 1974; Howe *et al.*, 1981; Ditchkoff and Mayer, 2009; Ballari and Barrios-Garcia, 2014). Rooting by pigs can reduce plant biomass, alter plant community composition, reduce plant and animal diversity, and facilitate invasion of nonnative plant species (Mayer, 2009a; Barrios-Garcia and Ballari, 2012). The impacts of wild pigs can vary depending on community type, vegetation structure and composition, type and availability of food, soil moisture, and size of the pig population (*e.g.*, Engeman *et al.*, 2007; Hayes *et al.*, 2009, Jolley *et al.*, 2010; Siemann *et al.*, 2009). No studies have examined the effects of wild pigs on plant and salamander communities in High Elevation Seeps.

Eurasian wild boar were originally introduced to the southern Appalachians in 1912 at a game reserve on Hoopers Bald in Graham County, North Carolina (Mayer, 2009b). These animals escaped into the wild and interbred with already existing feral hogs and free-ranging domestic swine to produce the wide-ranging phenotypes of wild pigs that are found in the region today (Mayer, 2009b). Although population numbers are unknown, wild pigs continue to proliferate throughout the southern Appalachians, and are well established in the mountains of North Carolina and Tennessee (Mayer, 2009b).

In the southern Appalachian Mountains, wild pigs prefer Northern Hardwood Forests during April through August and tend not to spend much time in Spruce-Fir Forests (Bratton, 1975; Howe and Bratton, 1976; Howe *et al.*, 1981). Therefore, the focus of this study is Rich Montane Seeps, because the integrity of this High Elevation Seep community is likely at the greatest risk of being threatened by wild pigs. Our objectives were to describe the abiotic and biotic attributes and evaluate the condition of Rich Montane Seeps where wild pigs are known to occur. In addition we: (1) estimated levels of pig disturbance within seeps; (2) examined the effects of wild pigs on plant and salamander communities; and (3) investigated how habitat attributes influence pig disturbance.

METHODS

STUDY AREA

Our study was conducted in the Great Smoky Mountains National Park (GSMNP; 35° 35′ N, 84° 30′ W), which is approximately 24 km from the epicenter of the original introduction of wild pigs to the southern Appalachian Mountains (Stiver and Delozier, 2009). The Park encompasses 2080 km^2, straddling the border of eastern Tennessee and western North Carolina. Because of its biological importance and high species diversity, GSMNP was designated an International Biosphere Reserve in 1976 and a World Heritage Site in 1983. Elevations in the Park range from 267 to 2025 m, and its topography can be characterized as rugged mountain terrain (Jenkins, 2007). The geology and the soils of the Park are complex and highly variable. The bedrock is dominated by metamorphosed sandstone, but acid-bearing slates, mafic and ultramafic rock, and tectonic windows underlain with limestone also occur (Southworth *et al.*, 2005). Annual precipitation ranges from 140 cm at low elevations to over 200 cm at high elevations (Jenkins, 2007). The Park has had an established wild pig control program since 1959 (Stiver and Delozier, 2009). Current population estimates of wild pigs in the Park range from 500 to 1000 animals, with the eastern half of the Park containing fewer pigs than the western half (B. Stiver, GSMNP, pers. comm.).

SAMPLE SITE SELECTION

To maximize the distribution of samples, the Park was divided into four quadrants and an attempt was made to sample during an equal number of days in each quadrant. Natural resource professionals and Park staff were consulted to help determine known locations of Rich Montane Seeps. We also used GIS data to narrow search areas and exclude areas of Spruce-Fir Forest. Final selection of sample areas was based on a variety of factors, including known location of seeps, access via trails or roads, and probability of encountering seeps based on topographic features such as slope and presence of streams.

A Rich Montane Seep was defined as any wetland with sheet flow occurring in hardwood forests above 1067 m (3500 feet). Only seeps > 15 m in length were sampled (*i.e.*, minimum length for inclusion of three plots, *see* details below). Samples were limited within a drainage basin (*i.e.*, an individual cove delineated by ridges on both sides) to the first three seeps encountered to reduce potential bias of location on wild pig effects and to increase the number of drainages sampled.

FIELD METHODS

Seeps were sampled from 5 June to 3 July, 2014. For each seep length and maximum width were measured, and slope and aspect were recorded. A transect placed on the longest axis of each seep was used to measure pig disturbance and habitat characteristics. Plots were centered every 5 m on the transect, with end plots located at least 2.5 m from the seep boundary to minimize edge effects. The number of plots sampled within a seep was determined by its length, with three being the minimum number to meet the acceptable size criteria of seeps as described above. Sampling was limited to 10 plots per seep to maximize sampling efficiency and because this sampling effort essentially captured all the herbaceous species in the plant community.

One meter-square plots were used to visually estimate percent pig disturbance; percent total plant cover (plants <0.5 m in height); percent plant cover by species (plants <0.5 m in height, with each species categorized in one of seven cover classes: <1%, 1–5%, 6–10%, 11–25%, 26–50%, 51–75%, 76–100%); plant richness (number of species <0.5 m in height); percent surface water; and percent substrate in each of five size classes: soil and sand (<2 mm), gravel (2–65 mm), cobble (66–250 mm), boulder (>250 mm), and bedrock (modified from Rosgen, 1996). In each plot diameter (>2.5 cm) and length of all down woody debris were also measured using a Biltmore stick to calculate volume. Percent pig disturbance was based on the total amount of surface area disturbed in the 1-m^2 plots and included surface and subsurface rooting, as well as areas used for wallows and trails. No attempt was made to determine how old the disturbance was. The presence of wild pigs was confirmed by tracks and other field sign (Mayer, 2009c). Circular plots with a 3 m diameter (using the same center point as the 1-m^2 plots) were used to record shrub density by species (number of woody stems >0.5 m in height and <2.5 cm diameter) and to measure the diameter-at-breast-height (dbh) of all trees (≥2.5 cm dbh). An inventory of vascular plants was conducted in each seep by walking the site and recording all plant species not accounted for in the 1-m^2 plots.

SALAMANDER SAMPLING

Salamanders were sampled in each of the 1-m^2 plots after the vegetation was sampled. Sampling entailed searching under all cover objects within the plot. All salamanders observed in the plot were counted, whether they were captured or not, to estimate surface density. All captured animals were placed in individual plastic bags during sampling to reduce the chance of double counting individuals on a plot, identified to species when possible, and classified as larva, juvenile or adult. Diagnostic keys provided by Petranka (1998) were used to help identify species for larvae and adults. Total Length (TL) of salamanders described in Petranka (1998) was used to classify species as juvenile or adult. All captured salamanders were released after each plot was sampled.

DATA ANALYSIS

Overall Importance Values (IV) were calculated for each plant species occurring in the 1-m^2 plots to describe the contribution of each plant within the entire seep community (Barbour *et al.*, 1998). The midpoint of each cover class was used to estimate total cover of each species (Peet *et al.*, 1998). The IV of each species was calculated using the equation:

IV = relative cover of a species + relative frequency of a species where: relative cover = total cover of a species / total cover of all species, and relative frequency = number of plots in which a species occurs / total number of plots (Ellum *et al.*, 2010).

Linear mixed models (LMM) were used to examine the effect of pig disturbance (fixed effect) on total plant cover (response variable) and plant richness (response variable). A generalized linear mixed model (GLMM) was used to examine the effect of pig disturbance (fixed effect) on salamander surface density (response variable). Habitat attributes were included as fixed effects in the mixed models so that they could be adjusted for when examining effects of wild pigs. Seep and drainage were considered random effects in each model to account for potential autocorrelation among variables and to avoid pseudoreplication. Because salamander surface density was a count variable, a Poisson distribution was used. No correction for overdispersion was made because the estimated deviance (*i.e.*, generalized chi-square/degrees of freedom) was 1.24, close to the ideal value of one. Although plant richness was also a count variable, the Poisson distribution was not used because residual plots indicated the spread of the residuals did not increase as the predicted values increased. Residuals of the LMMs for total plant cover and plant richness were positively skewed due to two outliers, so the analysis was redone with those plots removed. Removing the outliers improved the normality of the residuals but resulted in very minor changes in the results, so only the results with the full dataset are reported. The Kenward-Rodger procedure was used to estimate error variances and corresponding degrees of freedom for each model.

To examine how habitat attributes at the seep level affected pig disturbance a stepwise procedure using an alpha of 0.05 for variables to enter and leave the model was utilized to find a GLMM. Fixed variables in the analysis included slope, elevation, aspect, percent surface water, down woody debris, substrate type, and shrub and tree densities. Drainage was a random effect in the model. Means for percent pig disturbance, percent surface water, down woody debris, substrate type, and shrub and tree densities were calculated for each seep using the plot data. Mean pig disturbance was used as the response variable in the GLMM while the other variables were used as potential predictor variables. For all statistical analyses SAS version 9.2 was used and results were considered significant at alpha = 0.05.

RESULTS

SEEP CHARACTERISTICS

Thirty-five seeps, representing 24 drainages, were sampled across the Park. Forty-nine percent (N = 17) of seeps and 54% of drainages (N = 17) had some evidence of pig disturbance. Total amount of pig disturbance within seeps varied from 0-96% of the seep area (mean = 21%). Seeps were 1.5-16.4 m wide (mean = 7.6 m) and 15-266 m long (mean = 54 m). Their size ranged from 75 to 3804 m^2 (mean = 490 m^2), and they occurred on slopes ranging from 1 to 48% (mean = 17%). Substrates were generally comprised of a mixture of soil and sand, gravel, and cobble, which constituted over 90% of the total substrate (Table 1). However, a few seeps were composed almost entirely of mucky soils (N = 3), while others contained numerous large boulders (>40% of seep), characteristic of a boulder field (N = 2).

PLANT COMMUNITY AND PIG EFFECTS

Plant cover and plant richness differed among seeps (N = 35, both $P < 0.03$), but not among drainages (N = 24, both $P > 0.05$). One hundred eighty species of plants were recorded in the seeps, including 132 species of herbs, 35 species of shrubs, and 13 species of trees (Appendix 1). Mean total plant cover in the herbaceous layer was 44.6%, with a mean of 6.28 species/m^2 (Table 1). Woody plants in the shrub and tree layers were intermittently scattered throughout the seeps and occurred at low densities (Table 1, Appendix 2). Several herbaceous species were dominant across seeps, including (in order of importance): wood nettles (*Laportea canadensis*), branch lettuce (*Micranthes micranthidifolia*), turtlehead (*Chelone* sp.), scarlet beebalm (*Monarda didyma*), pale jewelweed (*Impatiens pallida*), foamflower (*Tiarella cordifolia*), white wood aster (*Eurybia divaricata*), and green-headed coneflower (*Rudbeckia laciniata*; Appendix 1).

TABLE 1.—Amount of pig disturbance and habitat attributes of 35 Rich Montane Seeps in the Great Smoky Mountains National Park, June 5 – July 3, 2014

Variable[a]	Mean	SE	Range
Pig Disturbance (%)	24.7	2.5	0–100
Plant Richness (species/m^2)	6.28	0.20	1–14
Total Plant Cover (%)[b]	44.6	2.2	0–100
Surface Water (%)[b]	26.0	1.9	0–100
Soil and Sand (%)	53.8	2.5	0–100
Gravel (%)	18.8	1.5	0–95
Cobble (%)	18.0	1.4	0–90
Boulder (%)	7.8	1.1	0–80
Bedrock (%)	1.7	0.7	0–100
Down Woody Debris (cm^3/m^2)[b]	15826	4044	0–644675
Shrub Density (stems/m^2)[c]	0.144	0.015	0–1.33
Tree Density (stems/m^2)[c]	0.022	0.003	0–0.22
Larval Salamander Density (no./m^2)	0.061	0.026	0–5
Juvenile Salamander Density (no./m^2)	0.899	0.103	0–13
Adult Salamander Density (no./m^2)	0.412	0.047	0–4
Total Salamander Density (no./m^2)	1.372	0.120	0–13

[a] Data are from 228, 1-m^2-plots, except as noted below
[b] Total Plant Cover and Down Woody Debris data are from 227 plots, and Surface Water data are from 226 plots
[c] Data are from 228, 3-m-diameter circular plots

Forbs represented the most important group of plants in the herbaceous layer accounting for 72% of the total IV, followed by bryophytes (mosses and liverworts, 17%), woody plants (shrubs, trees, and vines; 6%), and graminoids (grasses and sedges, 5%; Appendix 1). Seeps included eight plants of conservation concern: nerved sedge (*Carex* cf *leptonervia*; NC watch list); Ruth's sedge (*Carex ruthii*; NC watch list, TN threatened); golden-saxifrage (*Chrysosplenium americanum*; NC watch list); Virginia waterleaf (*Hydrophyllum virginianum*; TN threatened), purple fringed orchid (*Platanthera psycodes*; TN special concern), Rugel's ragwort (*Rugelia nudicaulis*; NC significantly rare, TN endangered), Clingman's hedge-nettle (*Stachys clingmanii*; NC watch list, TN threatened); and ramps (*Allium tricoccum*; TN special concern; Crabtree, 2014; Robinson and Finnegan, 2014).

Wild pigs had a negative effect on total plant cover (df = 139, $t = -6.67$, $P < 0.0001$) and plant richness (df = 144, $t = -3.61$, $P = 0.0004$). The regression coefficient for pig disturbance related to total plant cover was -0.4265, and the regression coefficient for pig disturbance related to plant richness was -0.02606. This indicates that for every 1% increase in pig disturbance, total plant cover is expected to decrease by 0.4265% and the number of plant species is expected to decrease by 0.02606%.

SALAMANDER OCCURRENCE AND PIG EFFECTS

Salamander surface density did not differ among seeps (N = 35, P = 0.08) or among drainages (N = 24, P = 0.39). A total of 315 salamanders, representing 10 species was recorded (Table 2), including three species of conservation concern: the southern pygmy salamander (*Desmognathus wrighti*; federal species of concern, NC state rare, TN species of special concern), the imitator salamander (*D. imitator*; NC watch list), and the Santeetlah dusky salamander (*D. santeetlah*; NC watch list, TN species of special concern; Withers, 2009; LeGrand *et al.*, 2014). Mean surface density of salamanders was 1.37 animals/m^2, with

TABLE 2.—Number of salamanders observed in 228, 1-m^2- plots in 35 Rich Montane Seeps in the Great Smoky Mountains National Park, June 5 – July 3, 2014

Species	Larva	Juvenile	Adult	Total
Black-bellied Salamander (*Desmognathus quadramaculatus*)	0	8	9	17
Seal Salamander (*Desmognathus monitcola*)	2	26	6	34
Imitator Salamander (*Desmognathus imitator*)	0	8	4	12
Ocoee Salamander (*Desmognathus ocoee*)	0	13	3	16
Southern Pygmy Salamander (*Desmognathus wrighti*)	0	0	3	3
Blue Ridge Two-lined Salamander (*Eurycea wilderae*)	4	28	0	32
Spring Salamander (*Gyrinophilus porphyriticus*)	1	2	2	5
Red-cheeked Salamander (*Plethodon jordani*)	0	0	1	1
Desmognathus santeetlah complex[a]	0	55	42	97
Desmognathus spp.	7	56	26	89
Unknown	0	8	1	9
Total	14	204	97	315

[a] Because northern dusky salamander (*D. fuscus*) and Santeetlah salamander (*D. santeetlah*) hybridize extensively in the GSMNP (Petranka, 1998), *D. santeetlah* complex includes *D. santeetlah, D. fuscus,* and *D. santeetlah* x *fuscus* hybrids

a maximum density of 13 animals/m^2 (Table 1). Juveniles accounted for 64% (N = 204) of the salamanders, followed by adults (29%, N = 97) and larvae (7%, N = 14; Table 2).

Wild pigs negatively affected salamander surface density (df = 42.11, $t = -2.16$, P = 0.037). The regression coefficient for pig disturbance was − 0.0064, indicating that for every 1% increase in pig disturbance, it is expected that the natural log of the mean salamander density will decrease by 0.0064% (*i.e.,* the mean decreases by a factor of 0.9936).

HABITAT EFFECTS ON PIGS

Slope was the only habitat attribute that affected pig disturbance (df = 30.1, $t = -2.22$, P = 0.034). The regression coefficient for slope was − 0.8994, indicating that for every 1% increase in slope the amount of pig disturbance is expected to decrease by 0.8994%. No other effects on pig disturbance were found for any of the other habitat variables (all P> 0.05).

DISCUSSION

This is the first comprehensive study of Rich Montane Seeps. Our data indicate Rich Montane Seeps are small linear wetlands characterized by an open canopy, dense herbaceous vegetation, and few trees or shrubs (Table 1). Because attributes of high-elevation seeps have not been previously quantified, no direct comparisons for this community were possible. The only other seep community that has been quantitatively described is Forested Hillside Seep in Maine. Morley and Calhoun (2009) reported this community is also characterized by a dense herbaceous layer and few trees (mean tree density = 0.16 stems/m^2). However, Forested Hillside Seeps are generally smaller (range: 5-800 m^2, mean = 143), occur on gentler slopes (slope 8-12%), and contain less down woody debris (range: 2200-11500 cm^3/m^2, mean = 6700) than Rich Montane Seeps in our study (Table 1).

Our finding that 49% of Rich Montane Seeps had some evidence of pig disturbance suggests the integrity of this community is being compromised. Wild pigs were the primary source of disturbance in seeps. However, one seep had minor disturbance caused by black bear (*Ursus americana*) tearing apart down woody debris, and another had some soil disturbance from elk (*Cervus elaphus*) browsing on its periphery. The overall level of pig disturbance in our study (21%) was similar to what has been reported for other wet habitats. For example, overall pig disturbance was: 25% in seepage slopes on Eglin Air Force Base in Florida (Engeman *et al.*, 2007); 19% and 9% in cypress-tupelo swamps and bottomland hardwood forests, respectively, in the Congaree National Park in South Carolina (Zengel and Conner, 2008); and 29% in floodplain forests in the Big Thicket National Preserve in Texas (Chavarria *et al.*, 2007).

Rich Montane Seeps provided habitat for numerous plant species (Appendix 1), including eight species of conservation concern, one of which is an endemic to the GSMNP (Rugel's ragwort; Weakely, 2012). Heavily disturbed areas were often completely denuded of plants. The negative impacts of wild pigs on plant cover and species richness are well documented (*e.g.*, Bratton, 1975; Siemann *et al.*, 2009; Cole *et al.*, 2012; Barrios-Garcia *et al.*, 2014). Our finding that forbs accounted for 72% of the total importance value of seeps, suggests this group of plants may be the most vulnerable to pig disturbance. Similar conclusions were reached by Bratton (1974, 1975) for mesic herbs in high-elevation hardwood forests of the GSMNP. Mesic herbs are eaten by wild pigs and killed from mechanical disturbance of rooting (Bratton, 1975). Wild pigs are known to repeatedly disturb areas in high-elevation hardwood forests year after year, and often several times during a growing season (Howe *et al.*, 1981). Bratton (1974) reported that the consequences of continual pig disturbance on mesic herbs include a decrease in the number and abundance of species, alteration of species composition towards plants with deep or toxic roots, and possible local extinctions of the most sensitive species.

Our results indicated Rich Montane Seeps are important to a diversity of salamanders. Ten species were recorded, including three species of conservation concern, one of which is an endemic to the GSMNP and the immediate vicinity (*D. imitator*, Petranka, 1998). Stream-breeding *Desmognathus* spp. were the most abundant, comprising 85% of the total salamanders observed (Table 2). The mean surface density of salamanders in our study (1.37 animals/m^2) suggests that Rich Montane Seeps provide high-quality habitat, particularly for metamorphosed individuals (Table 1). Petranka (1998) reported that optimal habitat for *Desmognathus* spp. often supports 1-2 animals/m^2.

Wild pigs had a negative effect on surface density of salamanders but to a lesser extent than on plants. In heavily disturbed seeps, much of the salamander habitat was degraded, as the rock substrate was buried under the soils from pig rooting. However, in seeps that were lightly to moderately disturbed, rocks were often displaced, but still available as cover objects. Observations at some seeps suggested moderate pig disturbance had only minor effects on salamander surface densities, particularly those dominated by rocky substrates. This is exemplified by data from one seep, which was moderately disturbed by pigs (30%), but had the highest mean surface density of salamanders of all seeps (5.1 animals/m^2) and the highest surface density of salamanders of all plots (13 animals/m^2).

The negative impacts of sedimentation on stream salamanders are well documented (*e.g.*, Hartwell and Ollivier, 1998; Russell *et al.*, 2005; Ward *et al.*, 2008). Increased sedimentation reduces the amount of interstitial space between rocks in the streambed which is critical cover, nesting and foraging habitat for salamanders (Hartwell and Ollivier, 1998). Observations during our study strongly suggest that wild pigs can increase sedimentation in seeps and thereby reduce the interstitial space in the substrate when churning up the soils and rocks during rooting activities. Means and Travis (2007) postulated rooting by wild pigs was at least partially responsible for the extirpation of the southern dusky salamander (*D. auriculatus*) and the severe decline of the spotted dusky salamander (*D. cf. conanti*) on Eglin Air Force Base. They suggested wild pigs eliminated the larval habitat of these two salamanders by transforming the substrate of the seepage slopes from fine sediments to thick beds of organic matter. In contrast Singer *et al.* (1984) found pig rooting had no measurable effects on upland salamanders in Northern Hardwood Forests of the GSMNP.

Our finding that slope had a negative effect on pig disturbance suggests seeps on flatter ground are more attractive to pigs, and therefore more vulnerable to disturbance, than seeps on steep ground. Bratton (1975) also observed lower rooting intensity on steep slopes in high-elevation hardwood forests. We are uncertain of the reasons for this. However, seeps on flat terrain often have deeper and more highly-developed soils than seeps on steep slopes and therefore may contain a different suite of plants that is a more desirable food resource. Seeps on flat ground also may be easier to root in, as well as have a greater proportion of suitable area for wallowing.

No habitat effects were found for any seep attribute (*i.e.*, elevation, aspect, percent surface water, substrate type, down woody debris, or tree and shrub density) other than slope, suggesting these other variables have little effect on how pigs choose seeps. This is in contrast to Singer *et al.* (1984) and Zengel and Conner (2008) who both reported positive associations between down woody debris and pig rooting. Singer *et al.* (1984) reported that in highly disturbed areas, 67% of branches and logs >2.5 cm diameter had been moved by wild pigs, and another 10% had been broken apart during rooting. Zengel and Conner (2008) reported a positive correlation between coarse woody debris and pig rooting in the Congaree Swamp, and speculated that woody debris was related to abundance of food.

CONCLUSIONS

Our data indicate that Rich Montane Seeps provide unique and high-quality habitat for a diversity of plants and salamanders that occur at high elevations, including numerous rare and endemic species. Our results suggest that wild pigs are threatening the ecological integrity of Rich Montane Seeps throughout their range by negatively affecting the plant and salamander communities, particularly in seeps occurring on flat terrain. Because our study was conducted in the GSMNP, where an active hog control program has been established since 1959, the levels of pig disturbance in Rich Montane Seeps outside the Park may be even greater than our results indicate. Therefore, additional surveys are needed throughout the southern Appalachians where wild pigs are known to occur to further evaluate the condition of Rich Montane Seeps, and to identify the best examples of this rare community, so that protection measures can be implemented.

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APPENDIX 1.— Plant species occurring in herbaceous layer of 35 Rich Montane Seeps in the Great Smoky Mountains National Park, June 5–July 3, 2014. Importance Values (IV) calculated from plants occurring in 228, 1-m^2 plots. * Indicates species of conservation concern in North Carolina or Tennessee

Species	Relative cover (%)	Relative frequency (%)	IV (%)
Bryophytes			
Mosses and liverworts	19.608	13.98	33.58
Graminoids			
Agrostis sp.	0.007	0.07	0.08
Carex appalachica	0.024	0.07	0.09
Carex cf *crebriflora*	0.037	0.21	0.25
Carex debilis	0.020	0.21	0.23
Carex cf *laxiflora*	0.024	0.07	0.09
Carex leptalea var. *leptalea*	0.020	0.21	0.23
Carex cf *leptonervia**	0.098	0.21	0.31
Carex pensylvanica	0.057	0.14	0.20
*Carex ruthii**	0.824	0.28	1.10
Carex scabrata	0.756	0.63	1.39
Carex sp.	0.132	0.56	0.69
Carex stipata var. *stipata*	0.371	0.49	0.86
Carex styloflexa	0.051	0.07	0.12
Glyceria melicaria	1.239	0.84	2.08
Luzula acuminata var. *acuminata*	0.132	0.56	0.69
Poa autumnalis	0.520	0.63	1.15
Forbs			
Aconitum uncinatum	0.625	0.40	0.836
Actaea podocarpa	0.051	0.07	0.12
Actaea racemosa	0.561	0.42	0.98
Ageratina altissima var. *altissima*	1.273	1.40	2.67
Anemone quinquefolia	0.020	0.21	0.23
Angelica triquinata	0.817	1.12	1.94
Arisaema triphyllum	0.118	0.70	0.82
Athyrium asplenioides	0.152	0.42	0.57
Botrypus virginianus	0.051	0.07	0.12
Cardamine diphylla	0.203	2.10	2.30
Cardamine pensylvanica	0.057	0.42	0.48
Chelone lyonii	2.280	1.12	3.40
Chelone sp.	5.687	2.87	8.55

APPENDIX 1.—Continued

Species	Relative cover (%)	Relative frequency (%)	IV (%)
*Chrysospleniu americanum**	1.158	1.68	2.84
Circaea alpina ssp. *alpina*	0.095	0.63	0.72
Collinsonia canadensis	0.290	0.42	0.71
Cryptotaenia canadensis	0.014	0.14	0.15
Cuscuta sp.	0.027	0.28	0.31
Cystopteris protrusa	0.074	0.14	0.21
Danthonia spicata	0.014	0.14	0.15
Deparia acrostichoides	0.064	0.21	0.27
Dioscorea villosa	0.098	0.21	0.31
Diphylleia cymosa	1.972	0.84	2.81
Dryopteris intermedia	1.479	1.12	2.60
Dryopteris marginalis	0.024	0.07	0.09
Eurybia divaricata	2.935	4.12	7.06
Eutrochium purpureum	0.513	0.21	0.72
Eutrochium steelei	0.051	0.07	0.12
Festuca subverticillata	0.027	0.28	0.31
Galium triflorum	0.520	1.12	1.64
Helianthus microcephalus	0.007	0.07	0.08
Houstonia purpurea var. *purpurea*	0.034	0.35	0.38
Houstonia serpyllifolia	0.111	0.35	0.46
Hydrophyllum canadense	3.002	1.40	4.40
Hydrophyllum var. *virginianum**	0.844	0.140	0.98
Impatiens capensis	0.044	0.280	0.32
Impatiens pallida	2.307	5.31	7.62
Laportea canadensis	11.962	7.83	19.79
Ligusticum canadense	0.098	0.21	0.31
Listera smallii	0.007	0.07	0.08
Lycopus sp.	0.014	0.14	0.15
Micranthes micranthidifolia	7.342	3.00	10.34
Mitchella repens	0.074	0.42	0.49
Mitella diphylla	0.007	0.07	0.08
Monarda didyma	3.870	4.33	8.20
Nabalus altissimus	0.155	0.91	1.06
Oclemena acuminata	0.014	0.14	0.15
Osmorhiza claytonii	0.226	0.56	0.79
Oxalis violacea	0.081	0.84	0.92
Persicaria sagittata	0.007	0.07	0.08
Phacelia fimbriata	0.007	0.07	0.08
Phlox stolonifera	0.125	0.14	0.26
Pilea pumila	0.898	0.56	1.46
Platanthera clavellata	0.007	0.07	0.08
*Platanthera psycodes**	0.024	0.07	0.09
Podophyllum peltatum	0.024	0.07	0.09
Polygonatum biflorum var. *biflorum*	0.030	0.14	0.17
Polypodium virginianum	0.007	0.07	0.08
Polystichum acrostichoides	0.125	0.14	0.26
Potentilla simplex	0.024	0.07	0.09
Prosartes lanuginosa	0.054	0.21	0.26
Ranunculus recurvatus	0.132	0.84	0.97
Rudbeckia laciniata var. *laciniata*	4.262	1.26	5.52
*Rugelia nudicaulis**	0.142	0.14	0.28

APPENDIX 1.—Continued

Species	Relative cover (%)	Relative frequency (%)	IV (%)
Rumex sp.	0.051	0.07	0.12
Sedum ternatum	0.007	0.07	0.08
Solidago curtisii	2.364	2.52	4.88
Solidago patula	0.875	0.35	1.22
*Stachys clingmanii**	0.206	0.35	0.56
Stellaria pubera	0.503	1.61	2.11
Symphyotrichum cordifolium	0.051	0.07	0.12
Symphyotrichum puniceum	1.773	0.49	2.26
Symphyotrichum retroflexum	0.054	0.21	0.26
Thalictrum clavatum	0.486	1.05	1.53
Thelypteris noveboracensis	1.672	1.12	2.79
Tiarella cordifolia	2.722	4.54	7.26
Trautvetteria caroliniensis	0.686	1.54	2.22
Trifolium pratense	0.007	0.07	0.08
Trillium erectum	0.267	0.56	0.83
Uvularia grandiflora	0.007	0.07	0.08
Uvularia perfoliata	0.007	0.07	0.08
Veratrum viride	0.304	0.14	0.44
Viola blanda	1.283	1.75	3.03
Viola cucullata	1.074	2.38	3.45
Viola pubescens	0.068	0.35	0.42
Viola sp.	0.007	0.07	0.08
Shrubs			
Clethra acuminata	0.024	0.07	0.09
Cornus alternifolia	0.118	0.07	0.19
Euonymus obovatus	1.223	2.31	3.53
Hydrangea arborescens	0.176	0.21	0.39
Kalmia latifolia	0.024	0.07	0.09
Rhododendron maximum	0.402	0.28	0.68
Rubus allegheniensis	0.709	0.70	1.41
Rubus canadensis	0.051	0.07	0.12
Sambucus canadensis	0.169	0.14	0.31
Vaccinium erythrocarpum	0.074	0.14	0.21
Vaccinium simulatum	0.057	0.14	0.20
Trees			
Acer rubrum	0.375	1.05	1.42
Acer saccharum	0.024	0.07	0.09
Acer sp.	0.007	0.07	0.08
Aesculus flava	0.047	0.14	0.19
Betula alleghaniensis	0.054	0.21	0.26
Fagus grandifolia	0.024	0.07	0.09
Fraxinus americana	0.446	0.98	1.42
Liriodendron tulipifera	0.024	0.07	0.09
Nyssa sylvatica	0.024	0.07	0.09
Pinus strobus	0.014	0.14	0.15
Prunus serótina	0.014	0.14	0.15
Quercus rubra	0.054	0.21	0.26
Vines			
Isotrema macrophyllum	0.132	0.21	0.34
Smilax rotundifolia	0.030	0.14	0.17

Species encountered outside of plots

Graminoids

Agrostis hyemalis
Carex aestivalis
Carex bromoides
Carex lurida
Carex plantaginea
Carex venusta
Glyceria striata
Juncus cf. *subcaudatus*
Juncus effusus ssp. *solutus*
Luzula sp.

Forbs

*Allium tricoccum**
Arnoglossum reniforme
Asplenium sp.
Astilbe biternata
Caulophyllum thalictroides
Cypripedium acaule
Goodyera pubescens
Heliopsis helianthoides
Lilium superbum
Maianthemum racemosum
Medeola virginiana
Osmundastrum cinnamomeum
Oxalis violacea
Oxypolis rigidior
Packera aurea
Persicaria virginiana
Scutellaria elliptica
Solidago sp.
Symphyotrichum retroflexum
Thalictrum sp.
Trillium grandiflorum

Shrubs

Leucothoe fontanesiana
Ligustrum sinense
Viburnum cassinoides
Viburnum lantanoides

Trees

Acer spicatum
Halesia tetraptera
Magnolia fraseri
Tsuga canadensis
Trillium undulatum
Veratrum parviflorum
Zizia aurea

APPENDIX 2. Density of woody plants in the shrub layer (plants >0.5 m in height and <2.5 cm diameter) and trees (≥2.5 cm dbh) in 35 Rich Montane Seeps in the Great Smoky Mountains National Park, June 5–July 3, 2014. Densities calculated from plants occurring in 228, 3-m-diameter circular plots

Species	Stems/m^2
Shrub layer	
Acer pensylvanicum	0.004
Acer rubrum	0.015
Acer saccharum	0.003
Acer spicatum	0.004
Aesculus flava	0.016
Amelanchier arborea	0.001
Betula allegheniensis	0.010
Betula lenta	0.001
Castanea dentata	0.001
Clethra acuminata	0.025
Cornus alternifolia	0.004
Fagus grandifolia	0.006
Fraxinus americana	0.040
Hamamelis virginiana	0.013
Hydrangea arborescens	0.054
Kalmia latifolia	0.026
Leucothoe fontanesiana	0.006
Liriodendron tulipifera	0.001
Prunus serotina	0.003
Pyrularia pubera	0.014
Quercus rubra	0.003
Rhododendron calendulaceum	0.003
Rhododendron maximum	0.064
Rubus allegheniensis	0.026
Rubus canadensis	0.001
Salix sericea	0.001
Sambucus canadensis	0.033
Tilia americana	0.004
Tsuga canadensis	0.004
Vaccinium erythrocarpum	0.026
Vaccinium simulatum	0.016
Viburnum cassinoides	0.001
Viburnum lantanoides	0.016
Trees	
Acer rubrum	0.007
Acer saccharum	0.004
Acer spicatum	0.001
Aesculus flava	0.023
Betula allegheniensis	0.012
Betula lenta	0.001
Cornus alternifolia	0.001
Fagus grandifolia	0.001
Hamamelis virginiana	0.001
Liriodendron tulipifera	0.001
Tilia americana	0.001
Tsuga canadensis	0.003