WINTER IS COMING: THE ECOLOGICAL DRIVERS OF *PHOTINUS CORRUSCUS (*COLEOPTERA: LAMPYRIDAE) DISTRIBUTION IN WESTERN NORTH CAROLINA

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By

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ABSTRACT

WINTER IS COMING: THE ECOLOGICAL DRIVERS OF *PHOTINUS CORRUSCUS (*COLEOPTERA: LAMPYRIDAE) DISTRIBUTION IN WESTERN NORTH CAROLINA
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The winter firefly, *Photinus corruscus* (Linnaeus, 1767), is a diurnal species commonly found throughout Eastern North America. This species has unique ecology – adults diapause through the winter on the sunny side of trees, whereas most other fireflies overwinter as larvae. However, because *P. corruscus* is dark (i.e., has no lanterns), this species has been studied less than its flashy relatives. Even basic aspects of its biology, such as its Hutchinsonian niche, sex ratio, and degree of gregariousness, remain unknown. *Photinus corruscus* is commonly found in Southern Appalachia, a mountainous region with diverse ecozones and a temperate climate. However, the spatial and seasonal distribution of *P. corruscus* were never studied in this region. This information is crucial to clarify the environmental conditions needed for survival and maintenance of *P. corruscus* and inform strategies for the conservation of *P. corruscus*. My study investigated the ecology of P. *corruscus* across the heterogenous landscape of Southern Appalachia by (I) exploring the ecological drivers of occurrence and abundance, and (II) measuring population ecological parameters, including sex ratio and gregariousness, to better understand the spatial and seasonal distribution of this species. I explored the correlation between 10 environmental variables over 12 sites across different ecozones to see how they influenced the occurrence and abundance of *P. corruscus* populations, which were collected with malaise traps sampled every two weeks. Individuals were found in 9 of 12 sites, starting from

February 2021 and ending in August 2021, with the highest abundance recorded at the end of April 2021. My results show that *P. corruscus* can survive across a wide range of environmental settings in Western North Carolina, as expected by its broad geographical range. A parametric model explained a major fraction (adjusted r^2 = 67%) of the total spatial variation in the local abundance of *P. corruscus* across sites. Moreover, a parametric model explained a relatively smaller portion (adjusted r^2 = 38%) of the total temporal variation across the sampling months. Winter fireflies were more abundant in warmer areas with moderate levels of humidity, larger trees spaced further apart, and exposed canopy cover during the winter. Adults were more active in late spring. Populations of *P. corruscus* were highly gregarious, with a male-biased sex ratio. Of 102 individuals collected, 68 were males and 34 were females. The biased ratio observed could result from females flying less often than the males (i.e., a sampling artifact), or less likely, from females having a lower survival rate than males. Furthermore, *P. corruscus* is locally gregarious, which is seen in nocturnal fireflies and could be a byproduct of potential mates gathering during the breeding season, and/or a strategy to maximize warning signals against visually oriented predators; both phenomena are widespread in closely-related firefly taxa.

INTRODUCTION

Fireflies are usually remembered as nocturnal flashers that swarm on warm summer nights, when males court their females (reviewed in Lewis & Cratsley, 2008). These charismatic insects feature textbook examples of sexual selection, in which females choose among several males by their flashy courtship displays, usually related to seminal nuptial gifts (Lewis & Cratsley, 2008). However, not all fireflies are nocturnal nor summer specialists (Faust, 2017; Silveira & Mermudes, 2017; Silveira et al, 2020). In fact, the more than 2,200 firefly species exhibit a vast array of interesting ecology and are often highly specialized in terms of habitat and seasonality (e.g. Silveira et al, 2020). Moreover, several species are not bioluminescent in the adult stage – instead, diurnal, dark fireflies, such as *Lucidota* and *Pyropyga*, rely more on sex pheromones to communicate with potential mates (Ming & Lewis, 2010)

Unfortunately, a historical bias towards bioluminescent adults has rendered lantern-less fireflies relatively understudied. As such, even basic aspects of their biology, like their environmental requirements, spatial clustering, and sex ratios, have rarely been studied (Rooney & Lewis, 2000; Faust, 2017; Ming & Lewis, 2010). For example, one of the most common diurnal and dark (i.e. lantern-less) fireflies found throughout Eastern North America, the winter firefly *Photinus corruscus* (Linnaeus), 1767, is comparatively poorly known.

Photinus corruscus is a large (9mm–18mm) lantern-less firefly (Faust, 2017). Recent phylogenetic work (Stanger-Hall et al, 2007; Stanger-Hall & LLoyd, 2015; Martin et al, 2019) revealed that *P. corruscus* is close to *Photinus pyralis*, a nocturnal, summer-adapted species that uses flash patterns in the adult stage to communicate with potential mates (Faust, 2017). Unlike *P.*

pyralis, in which the adults associate with warmer temperatures, *P. corruscus* is associated with cooler temperatures, more commonly seen flying early in spring (Faust, 2017).

As their common name suggests, *P. corruscus* emerge from the pupa stage and overwinter as adults to become active once again during early spring (Ronney & Lewis, 2000). When adults emerge, they crawl up the south side of the tree, which is the warmest side of the tree, and wedge their bodies into the grooves of the bark. After they have become stationary in the grooves of the bark, they will go into torpor, decreasing their metabolism (Ronney & Lewis, 2000). *Photinus corruscus* adults are thought to rely more on pheromones to find mates than flashing fireflies (Ronney & Lewis, 2000; Faust, 2012).

P. corruscus has a wide distribution (Fig. 1) and can be found from northern Quebec south to peninsular Florida, and west to Manitoba and Louisiana. Within the firefly's range, researchers have observed phenotypic variation, mostly in size (Faust, 2017; Ronney, 2000). This phenotypic variation could be the result of several different factors. First, *P. corruscus* may be a species complex, with multiple cryptic species being grouped as one species (Faust, 2017; Struck et al, 2018). Alternatively, this phenotypic variation could be the result of local adaptations. If local adaptations are the cause, there might be blocks in gene flow due to unusable habitats between populations. Thus, mapping the suitable habitats for *P. corruscus* is important to understand the species range and provide data for future investigations of ecological differences among species in this presumed complex. However, this is currently not possible because *P. corruscus* environmental requirements have never been previously measured.

Fig. 1 *Photinus corruscus* known distribution across temperate Eastern North America. (Faust, 2017; Ronney, 2000).

The ecological niche of a species includes the environmental requirements for its populations to grow and the biotic interactions that take place in the ecosystem (Hirzel & Lay, 2008). Populations are spatially and temporally dynamic, so understanding the factors that influence these dynamics can aid in managing populations. For example, by documenting the environmental requirements of a species, one can build a species distribution model (SDM) to map suitable habitats a species could survive in and anticipate the impact of one or more stressors on its distribution (Vaz, 2020). However, studying the niche of poorly known species is particularly challenging due to a lack of information on which environmental variables to analyze (Soberón, 2007). As such, one must choose a set of abiotic variables presumed to affect their target species over spatial and temporal dimensions based on their biology and/or comparison with better-known, closely related species (Soberón, 2007).

The variables driving the distribution and abundance of a species might vary with its ontogeny or developmental stages. Consider the fireflies of the genus *Photinus*: they often spend a few weeks in the egg stage, less than a year in the larval stage, 1-3 weeks in the pupa stage, and less than 1 month in the adult stage (Faust, 2017; Riley et al, 2021). The adults are winged and soft-bodied, which will render them rather prone to water loss, whereas larvae are hard-bodied and dwell in the leaflitter. Therefore, it is reasonable to predict that leaflitter density will be more relevant for the larvae than for the adults, and that relative air moisture should impact the latter more than the former. Taken together, all these variables contribute to a better model of a species' distribution.

Nocturnal firefly species are known to have gregarious distributions as they use lanterns in the adult stage to either flash or glow in order to communicate to potential mates (Lewis & Cratsley, 2008). However, there tends to be a male-biased sex ratio, leading to strong sexual

selection (Cratsley, 2005; Lewis, 1991; Barrows, 2008; Lewis & Cratsley, 2008). Documenting spatial clustering is therefore important because it is a basic population parameter and can provide insight on related, biologically relevant questions, like epidemiological issues, sexual behavior, and strategies to fend off predators (Deyrup et al, 2017; Lewis & Cratsley, 2008).

Depending on the species, the sex ratio, or relative proportion of males and females, varies spatially, temporally, and with age of individuals (Carmona-Isunza et al, 2017). The difference between males and females may limit reproductive success for each sex. The reproductive success of individual males increases with the number of successful mating events. Thus, males often achieve greater reproductive success by competing with other males to access as many females as possible, especially when females are rarer (i.e. in male-biased cohorts). Females invest more in each individual offspring and thus cannot produce as many offspring as males, but instead benefit from carefully choosing mates (Buunk & Fisher, 2009). However, in most sexually reproducing species the ratio tends to be 1:1 (Hamilton, 1967). For example, if the number of males is lower than the number of females, the male offspring will have a greater chance of finding mates. The process is reversed in favor of female offspring once they are outnumbered by the male offspring. Biased sex ratios can evolve under different conditions. These include sex competition and sex-specific dispersal, but also sex-specific symbiotic relationships (Buunk & Fisher, 2009). For example, competition between individuals of the same sex may cause a higher number of deaths of the corresponding sex (Buunk & Fisher, 2009). Sex-specific dispersal might also skew the sex ratio, including kin competition, inbreeding avoidance, and spatiotemporal variation in resources or habitat suitability (Li & Hanna, 2019). These factors differ in whether they promote male and female dispersal equally, and often selection on dispersal of one sex depends on how much the other sex disperses (Li & Hanna, 2019). For

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example, the dispersal of one sex away from the natal site can be crucial to avoid inbreeding (Li & Kokko, 2019). One byproduct of males and females gathering by means of dispersal is the creation of a gregarious distribution, also known as a clumped distribution.

To fill important gaps in the knowledge of *P. corruscus* biology, this study aimed to document *P. corruscus* spatial and temporal distribution, environmental drivers of abundance, spatial clustering, and sex ratio across different ecozones of the Southern Appalachians.

MATERIALS & METHODS

Study area and sites. The mountains of Western North Carolina are an ideal location to study *Photinus corruscus*'s environmental tolerances because the elevational gradients form diverse habitats at a relatively smaller spatial scale, encompassing a microcosm of the range of variation that is found throughout *P. corruscus* entire range. (Simon, 2005; and Spira, 2011; Faust, 2017). Specifically, I chose certain distinctive plant communities to incorporate their diverse characteristics (Simon, 2005; and Spira, 2011; Table 1). To assess how environmental variation shapes *Photinus corruscus* occurrence, I sampled 12 sites across Western North Carolina (eight sites in Jackson County and five in Macon County; Fig. 2, Table 1) to maximize spatial heterogeneity. Overall, these sites differ in temperature, air relative humidity, leaf litter density, soil moisture, canopy cover, throughfall, tree density, tree diameter, and nearest direct water source. Specifically, Balsam has spread out trees, steep slope, and moderately high humidity whereas Highlands Creek has closely-spaced trees, flat land, and high humidity. Tessentee, a hilled trail, with dense groundcover and trees scattered throughout the area. Both Despeaux estate locations also have dense open or dense shrubby or ??? vegetation, more so in the woodsy surroundings. The woods location is moderately dense with trees and has a river flowing through the ground. The pond on the other hand has a decently sized clearing on one side (pond side) and moderately dense trees on the other side. Wolf Creek is heavily vegetated and dark (due to the high canopy cover). Like Highlands Creek, Highlands woods has dense trees and a waterfall behind the malaise trap, but has a steep decline into the site. Laurel Knob rock outcrop is open with little ground cover and dense trees on one side of the trap. Brushy Face has dense trees and with deep leaf litter cover. WCU trail has a steep incline with moderately

closed canopy and dense vegetation. Unlike Laurel Knob, Satulah had bedrock on the trail

behind the trap but, overall, has less exposed rock and scattered trees. Lastly, High Falls Trail

has a stream cutting across the location with trees dispersed evenly and vegetation cover all

around the site.

Table. 1 Six distinctive Western NC plant communities sampled in this study and some of their environmental characteristics (Simon, 2005; and Spira, 2011).

Plant Communities	Elevation	Temperature Range (C°)	Precipation	Leaf Litter Density	Sampling Sites
Northern Hardwood	Above 1,219m	19c-22c	Low	Deep	Balsam, Tessentee, WCU Trail
Acidic Cove	Below 1,219m	4c-21c	High	Deep	High Falls, Despeaux's Estate [Pond]
Rich Cove	609m-1,219m	5c-21c	Moderate	Deep	Wolf Creek
Pine Oak Heath	304m-1,219m	21c-27c	Low	Moderate	Despeaux's Estate [Woodland]
High Elevation Red Oak	1,066m-1,676m	4c-16c	Low	Shallow	Highlands Creek, Highlands Woods, Brushy Face
High Elevation Rocky Outcrops	Above 1,070m	4c-18c	High	Shallow	Laurel Knob, Satulah
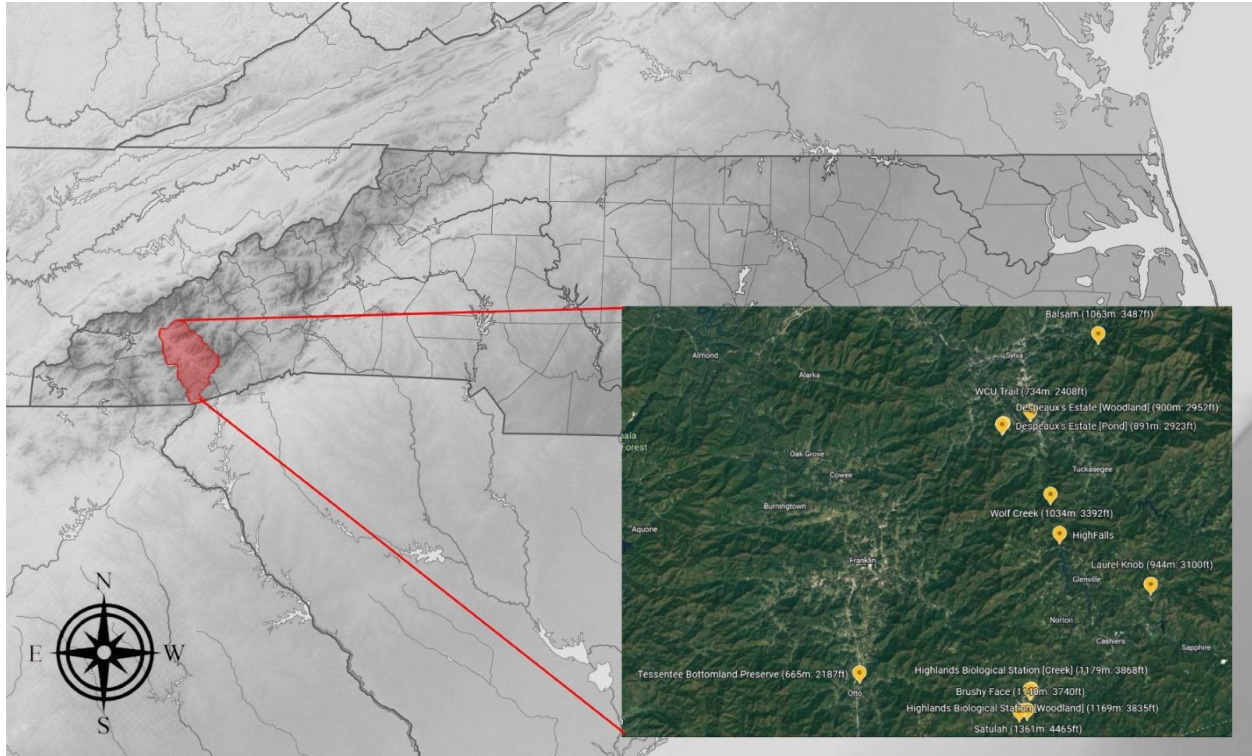
Fig. 2 Distribution of sampling sites in this study across Western North Carolina.

Experimental design. The *Photinus corruscus* breeding season starts in early March and ends in late May (Ronney & Lewis, 2000; Faust, 2012). To document the occurrence of *P. corruscu*s, 12 Townes-style malaise traps (Fig. 3) were deployed throughout Western North Carolina (Fig. 2). All 12 malaise traps were set up at the end of February (before *P. corruscus* breeding season started) and were taken down at the end of August. I kept the malaise traps up after *P. corruscus* breeding season because, based on museum collections data (Silveira, pers. ob.), *P. corruscus* can still be found throughout the summer.

Environmental sampling. Nine spatial and six temporal environmental variables were measured to document *Photinus corruscus* microhabitat preferences (Kristensen, 1999; Bouget, 2004). The nine spatial environmental variables were average temperature, air relative humidity, leaf litter density, soil moisture, canopy cover, throughfall, tree density, tree diameter, and nearest

direct water source. The six temporal environmental variables were average temperature, relative air humidity, leaf litter density, soil moisture, canopy cover, and throughfall. The temporal environmental variables were measured every two weeks, leaving tree density, tree diameter, and nearest direct water source to be measured once throughout the 6-month sampling period. These nine environmental variables were chosen because, in general, fireflies are sensitive to these variables (see Introduction above; Faust, 2017; Faust, 2010).

How these variables were decided was based on not only the adult stage of *Photinus corruscus* but also the larva stage. Larvae are presumed to be most affected by throughfall, leaf litter density, and soil moisture. These were chosen based upon the larva's quality of shelter and availability of prey, which are mostly earthworms, snails, and slugs (Riley et al., 2021). In contrast, flying adults should be more affected by temperature, humidity and distance to a direct water source because a body of water could aid in increasing humidity. Then lastly the canopy cover, tree density and tree diameter could directly affect overwintering *P. corruscus* adults.

Fig. 3 Townes-style malaise trap at High Falls sampling site, taken on 2/27/2021 at 12:45PM.

To measure these nine environmental variables, a 40m-by-40m plot centered at the malaise trap was created, which allowed me to gather more comprehensive measurements representing the area surrounding the trap. Due to the natural landscape, seven trap sites, (Despeaux's Estate [Pond], Laurel Knob, WCU Trail, Highlands Biological Station [Woodland], Highlands Biological Station [Creek], Satulah, and Brushy Face) had reduced plot size to allow for safely collecting the environmental measures. To complete the plot setup, I established a 40m-by-40m plot, broken into four smaller quadrants (20m-by-20m) centered around the malaise trap. Flags were placed 5m apart in each quadrant, for a total of four flags per quadrant and 16 total flags per plot.

Once the plots were created, temperature and relative air humidity were measured with Hygrochorn Ibuttons (manufacturer: iButtonLink Technology, Item Code: DS1923-F5). All Hygrochrons were placed roughly 10cm above the ground in order to measure air temperature and

humidity for adult *Photinus corruscus* rather than larvae air temperatures. Hygrochrons were put on the south side of the tree that contained the malaise bottle at each trap location.

All 16 flags were used to measure both leaf litter density and soil moisture. Leaf litter density was measured by using a pizza pan (33cm diameter) as a standard sampling unit; pans were randomly placed on the ground next to each of the 16 flags. A rake was used to separate the leaf litter matter from the outside surrounding the pizza pan from what was underneath. The pizza pan was lifted and any leaf litter matter under the pizza pan was placed into a labeled bag. Soil moisture was measured by using a Hydro-sense II (manufacturer: Campbell Scientific, Item Code: CS658). The 20cm probe rods were placed randomly in the ground within a meter to each of the 16 flags. At each flag the volumetric water content was calculated and recorded, as a surrogate for soil moisture.

Canopy cover was measured on all four sides (North, East, South, West) of the malaise trap with a Spherical Densitometer held at chest height. This pocket size instrument employs a mirror with spherical curvature, allowing one to see how much light is passing through the canopy. On the mirror a grid is used to calculate the percentage of how much space is exposed in the canopy. This percentage is calculated by counting how many corners in each square on the grid are exposed and multiplying the final count by 1.04, to get the exposed canopy cover percentage.

Throughfall relates to how much rainwater can penetrate the canopy and reach the ground. To measure throughfall homemade water gauges were created for all 12 sites. The top rim of a two-liter soda bottle was cut off and flipped upside down to act as a funnel. The bottle was strapped to a wooden stake, and the wooden stake was hammered into a random spot next to the malaise trap. Every two weeks I would return to the water gauge where the rainwater was collected and taken back to the lab to be measured by graduated cylinders.

Malaise traps are often built around trees because branches from trees are used to help strap down the trap and act as cover. Therefore, to measure tree density I used the point-centered quarter method, which allowed me to avoid trees holding the malaise traps (Mitchell, 2010). In this procedure two perpendicular transects were created at each of the 16 flags, thus breaking each individual flag into four sub quadrants. By using the flag as the starting point, I first measured the nearest tree [woody plant having a trunk and greater than 1.3m tall] to this flag and then measured the nearest tree to the tree nearest to the flag. Only the second distance recording was used to calculate tree density. To calculate tree density, I averaged the raw distance (davg) and used the formula $MA = (davg)^2$. After the MA has been calculated, I used the density formula Density= (1)/MA to calculate the density of trees. While measuring tree density I would calculate the tree diameter by measuring the circumference of the second nearest tree at 1.3m above the ground. To find the diameter I would take the circumference and divide it by π.

To record the distance to water source, I would use the malaise trap as the starting point, and would walk to the nearest body of water such as a creek, river, pond, stream etc. Once the nearest direct water source has been located, a tape measure was used to record the distance.

Sample collection. Abundance data for *Photinus corruscus* and *Photinus pyralis* (for abundance comparison; see below) were taken by searching through the 144 malaise bottles gathered at the end of the 6-month sampling period. *P. corruscus* and *P. pyralis* present in the malaise bottle were separated from the remaining by-catch and placed into a separate labeled container. To determine firefly sex, abdominal ventrites VI–VIII shape, which is sexually dimorphic (Marvin, 1965), was compared under a dissecting microscope. Specifically for *P. corruscus*, the female's terminal segment is shaped like a triangle while the males are rounded out (Marvin, 1965).

Statistical analysis. All analyses were conducted in R 3.3.2 (R core Team 2016). Abundance data were log-standardized by using the "decostand: log" function of the "vegan" package in R and checked for normality with a Shapiro-Wilk test. The environmental data were standardized by unit variance (decostand: standard).

Principal Component Analysis (PCA) based on a covariance matrix was used to summarize environmental data covariation (Antúnez, 2021). Meaningful PCA axis (i.e., those with eigenvalues higher than expected by chance) were determined via a parallel analysis of the randomized environmental matrix (Janžekovič & Novak, 2012). The resulting meaningful axis were used as independent variables in a Generalized Linear Model, then submitted to a likelihood-based model selection using the R package "MuMIn". To analyze how temporal and spatial variables impacted *P. corruscus* abundance, I used a linear regression, using the PCA scores as independent variables, and the log-transformed abundance counts as the dependent variables.

Recently, it was brought to light that *Photinus corruscus* is a close relative of the well-known *P. pyralis* (Stanger-Hall & Lloyd, 2015), a flasher species known to be locally gregarious (Faust, 2017; pers. obs.). Therefore, I compared the Dispersion indices (variance/average) as a surrogate for the spatial clustering of both species, calculated per site or sampling period. Figures were built with ggplot and ggord (Kindt, 2020).

Spatial analyses. A total of 102 *Photinus corruscus* individuals were caught in 9 of the 12 sampling sites (Table 2). Two sites, Balsam, with 53 individuals, and High Falls Trail, with 19 individuals, are potential outliers regarding *P. corruscus* spatial abundance. *P. corruscus* raw abundance data was skewed (Shapiro-Wilk's W= 0.59405, *p*= 0.00009574), but was normalized through log-transformation W= 0.93373, *p*= 0.4214) (Table 2).

Table. 2 Number of individuals *Photinus corruscus* captured in malaise traps per site location.

Site Location	# of *Photinus corruscus*
Balsam	53
Tessentee	7
Sloan Pond	4
Sloan Woods	2
WCU Trail	4
Wolf Creek	4
High Falls	19
Laurel Knob	8
Highlands Creek	0
Highlands Woods	0
Satulah	2
Brushy Face	0

Parallel analysis determined that PCA axis 1–3 was statistically significant (Table 3). The first PCA axis summarized 38.19% of the total covariance, the second axis accounted for 24.22%, and the third axis had 15.51% of the remaining covariance. The first axis was negatively correlated with humidity and tree density, and positively related to temperature, tree diameter, and distance

to water source. The second axis was negatively correlated with soil moisture and throughfall, and positively correlated with canopy cover, leaf litter density, and temperature. The third axis was negatively correlated with humidity, leaf litter density, throughfall, distance to water source, and was positively correlated with temperature, soil moisture, canopy cover, tree diameter, and tree density (Table 3).

The PCA revealed that Balsam (1), Tessentee (2), and WCU Trail (5) were the most similar to one another; they had the hottest temperatures, lowest humidity, and biggest trees that were spaced out (Fig. 4). High Falls Trail (7), Wolf Creek (6), Despeaux's Estate [Pond] (4), Despeaux's Estate [Woodland] (3) were similar to one another, with intermediate temperatures and smaller trees. Laurel Knob (8) had the least canopy cover with shallow leaf litter density and was the furthest site from a direct water source. Satulah (11), Highlands Woods (10), Highlands Creek (9), and Brushy Face (12) had the coolest temperatures, highest humidity, and highest soil moisture.
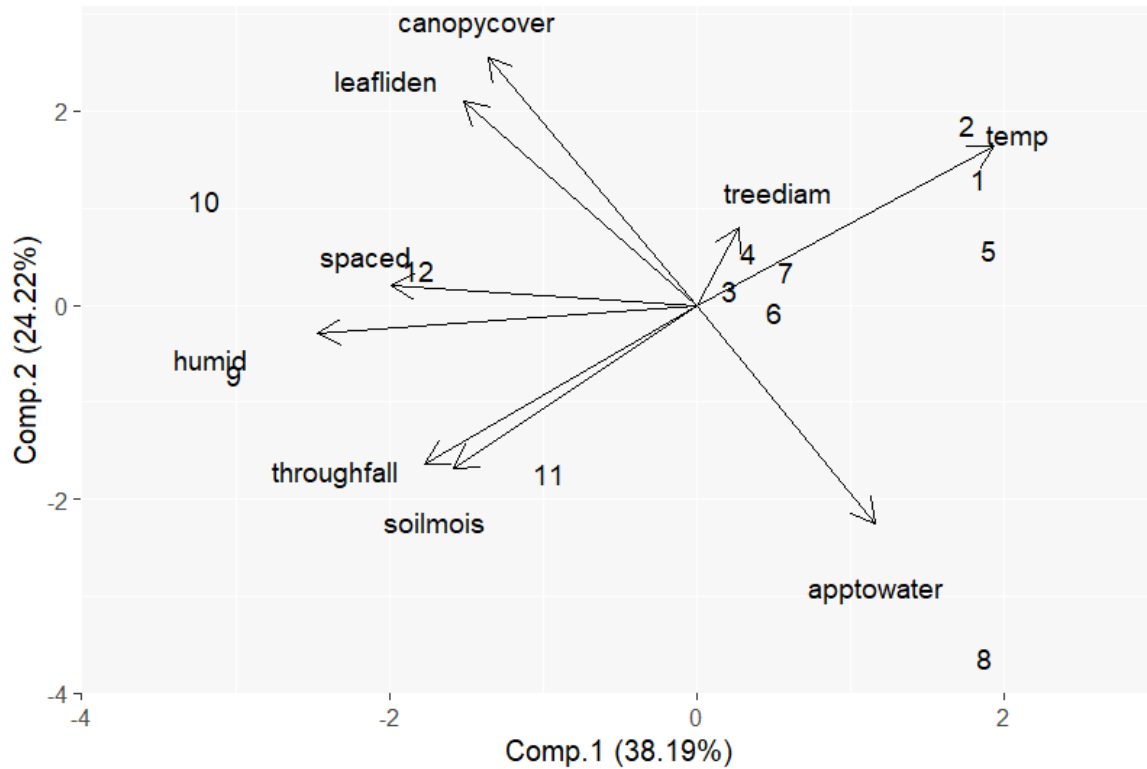
Fig. 4. Principal components analysis of 12 sites in WNC included in this study, summarizing ecological variables covariation. The component axis represents a combination of the environmental variables (Table 2), while the arrows represent the Eigenvectors Site labels: 1(Balsam), 2(Tessentee), 3(Despeaux's Estate [Pond]), 4(Despeaux's Estate [Woodland]), 5(WCU Trail), 6(Wolf Creek), 7(High Falls Trail), 8(Laurel Knob), 9(Highlands Biological Station [Creek]), 10 (Highlands Biological Station Woodlands), 11(Satulah), 12(Brushy Face). Abbreviations: Temp: temperature, humid: humidity, soilmois: soil moisture, throughfall: throughfall, leafliden: leaf litter density.

Table. 3 Loadings for the first three component axis of the spatial PCA showing the combinations of environmental variables for each axis.

Environmental Variables	Comp.1	Comp.2	Comp.3
Temp	0.386	0.327	0.141
Humid	-0.494	N/A	-0.233
Leafliden	-0.303	0.42	-0.18
Soilmois	-0.317	-0.338	0.373
Throughfall	-0.354	-0.328	-0.343
Canopycover	-0.272	0.512	N/A
Treediam	N/A	0.161	-0.699
Apptowater	0.232	-0.449	-0.222
Spaced	-0.398	N/A	0.308

Model selection based on multiple linear regression of PCA scores 1–3 against log-transformed *P. corruscus* abundance found that a sub model with axis 1 was a better fit model (Table 4). A sub model using the PCA scores from axis 1 (Table 4) had an adjusted R- squared of 0.679.

Table. 4 Results of the Model selection using meaningful spatial PCA scores (axis 1–3). A submodel with axis 1 performed significantly better. Abbreviations: df: degrees of freedom, logLik: extract log- likelihood, AICc: Akaike information criterion, delta: delta, weight: weight.

Model	df	logLik	AICc	delta	weight
Axis 1	3	-18.047	45.1	0	0.818
Axis 1 + Axis 3	4	-17.929	49.6	4.48	0.087
Axis 1 + Axis 2	4	-17.933	49.6	4.49	0.087
Axis 1 + Axis 2 + Axis 3	5	-17.813	55.6	10.53	0.004
No Axis	2	-25.437	56.2	11.11	0.003
Axis 3	3	-25.403	59.8	14.71	0.001
Axis 2	3	-25.404	59.8	14.71	0.001

Since the linear regression showed only axis 1 was significant in explaining which environmental variables correlated the most to *Photinus corruscus* abundance (Table 3), I examined the variable loadings on axis 1 (Table 3) to see which environmental variables contributed the most to the variance explained. *Photinus corruscus* abundances were positively correlated with temperature and negatively correlated with humidity and tree density.

Table. 5 Linear spatial regression model only using PCA scores from axis 1. Axis, one had a small standard of error and was significant. Axis one was positively correlated to the spatial PCA.

PCA 1	Standard Error	Correlation	Significance
Axis one	0.194	4.926	0.000599***
Adjusted R-Squared			0.679

Photinus corruscus abundance is significantly gregarious in the southern Appalachian region, as revealed by comparing *P. corruscus* dispersion index to *P. pyralis*, known to be gregarious (*P. corruscus*= 26.00088; *P. pyrali*s= 6.00000). *P. corruscus* temporal abundance is significantly clustered in the Southern Appalachian region, as revealed by comparing *P. corruscus* dispersion index to *Photinus pyrali*s (a known season-specialist species) (*P. corruscus*= 14.56222, *P. pyralis*= 9.455).

Temporal analyses. A breakdown of *Photinus corruscus* temporal abundance throughout the sampling sites can be seen in Fig. 5. *Photinus corruscus* raw temporal abundance was not normal (Shapiro-Wilk's W= 0.77919, *p*= 0.00486), but was normalized through log transformation (W= 0.92404, *p*= 0.3212). With *P corruscus* having a short breeding season, I would expect to see them evenly distributed together throughout the course of the year. However, *Photinus corruscus* abundance starts off low at the beginning of the year, and peaks in mid-May, with the majority of individuals collected from April 26th to May 10th, 2021 (37, 36.27% total). Throughout the summer *P. corruscus* can still be found, however by mid-August their occurrence drops off (Fig. 5).

Temporal Variation of Abundance
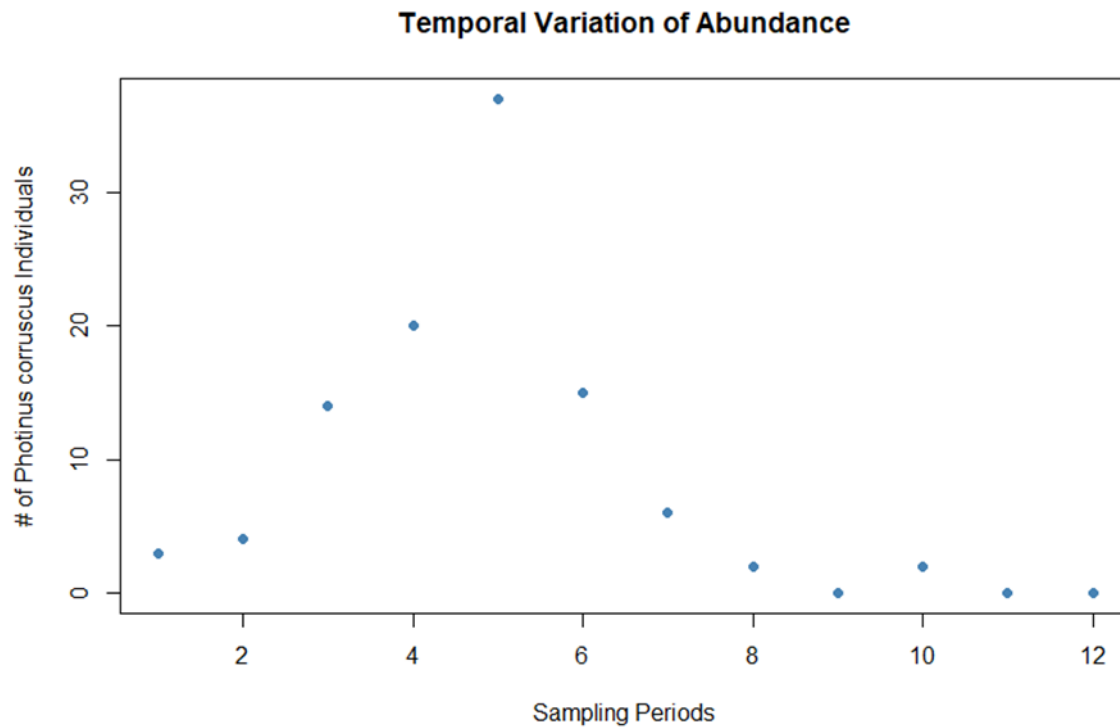
Fig. 5 *Photinus corruscus* raw temporal abundance, plotted as all individuals caught by sampling unit (i.e., biweekly) without transforming the data. The sampling unit labels are as follows: 1(2/27/21 - 3/15/21), 2(3/15/21 - 3/29/21), 3(3/29/21 - 4/12/21), 4(4/12/21 - 4/26/21), 5(4/26/21 - 5/10/21), 6(5/10/2021 - 5/24/21), 7(5/24/2021 - 6/7/21), 8(6/7/2021 - 6/27/21), 9(6/27/2021 - 7/11/21), 10 (7/11/2021 - 7/25/21), 11(7/25/2021 - 8/8/21), 12(8/8/2021 - 8/21/21).

In the temporal PCA of environmental variables, axis one accounted for 56.03% of the overall variation, while axis two accounted for 27.02% of the remaining variation. The start of the data period collections (mid-March through late April) were the coldest and driest times with the least canopy cover (Fig. 5), while the end of data period collections (mid-July through August) were the hottest and dampest humidity times with the most canopy cover. Mid- to late-May experienced the most throughfall with wettest soils.
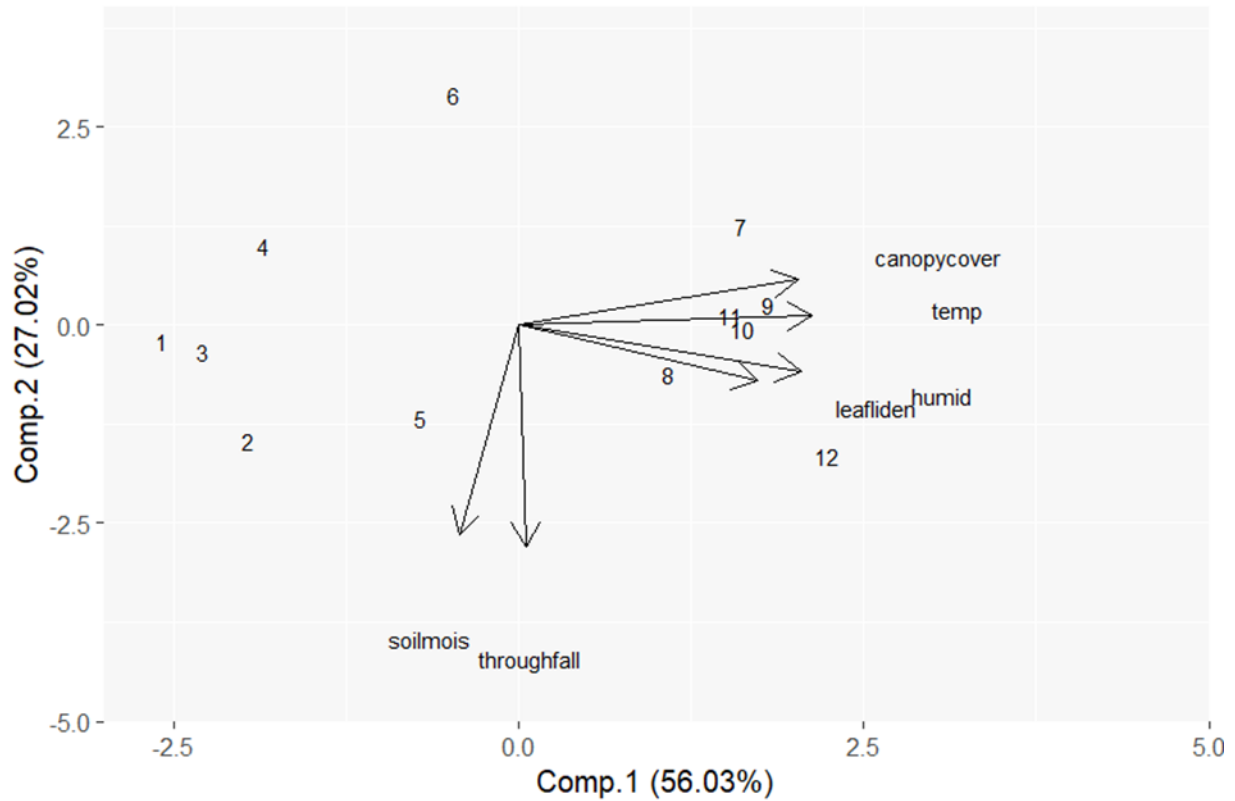
Fig. 6 Temporal principal component analysis (PCA) grouping site locations based upon similarities among environmental conditions over time. Each number is a sampling period (see fig 5). Abbreviations: Temp: temperature, humid: humidity, soilmois: soil moisture, throughfall: throughfall, leafliden: leaf litter density. Time Intervals: refer to table 6

Table. 6 Loadings for the first two component axis of the temporal PCA showing the combinations of environmental variables for each axis.

Environmental Variables	Comp. 1	Comp. 2
Temp	0.531	N/A
Humid	0.511	-0.147
Leafliden	0.433	-0.175
Soilmois	-0.108	-0.659
Throughfall	N/A	-0.701
Canopycover	0.507	0.143

The parallel analysis revealed that the first two PCA components axis should be retained for further analyses. A model selection of PCA scores from axis 1 and 2 against firefly abundances found that a model with axis 1 only performed better than the full model (Table 7). So, I ran a second linear regression model only using the PCA scores from axis 1 (Table 8). The complete linear regression model (axis 1 and 2) had an adjusted R- squared 0.4168, while the second linear regression model (axis 1 only) had an adjusted R- squared of 0.3843.

Table. **7** Model selection using PCA scores from axis 1 and 2. The first two axis had a small standard of error but only axis one was significant. Axis was negatively correlated to the temporal PCA and axis two was positively correlated with the temporal PCA. Abbreviations: df: degrees of freedom, logLik: extract log- likelihood, AICc: Akaike information criterion, delta: delta, weight: weight.

Model	df	logLik	AICc	delta	weight
Axis 1	3	-22.332	53.7	0	0.671
Axis 1 + Axis 2	4	-21.374	56.5	2.8	0.166
No Axis	2	-25.814	57	3.3	0.129
Axis 2	3	-25.297	59.6	5.93	0.035

After running the temporal model selection, the linear regression showed only axis 1 was significant in explaining which environmental variable over time correlated the most with *Photinus corruscus* abundance (Table 7), I examined the variable loadings on axis 1 (Table 6) to see which environmental variables contributed the most to the variance explained. *Photinus corruscus* abundances were positively correlated with temperature, humidity, leaf litter density, and canopy cover.

Table. 8 Linear temporal regression model using PCA 2 scores from axis 1.

PCA 2	Standard Error	Correlation	Significance
Axis 1	0.2803	-2.805	0.018647*
Adjusted R-Squared			0.3843

Sex ratio. A total of 68 males and 34 females were caught out of 102 total individuals, a significant deviation from an even distribution, as confirmed by a chi-square test (Chi=5.163, p=0.02).

DISCUSSION

***Photinus corruscus* environmental preferences.** This is the first quantitative assessment of the ecological niche of a dark firefly species in North America, and an important step towards its conservation and management. My data show that temperature, relative air humidity, tree density, soil moisture and throughfall were the most important predictors of spatial variation in *P. corruscus* abundances. My data are based on correlations, but I provide a few interesting explanations for the patterns observed, as follows.

It is widely known that insects, including most firefly species, tend to be more diverse in environments with higher levels of humidity (Tochen et al, 2016, Vaz, 2020). However, despite thriving in these mesic environments (Vaz, 2020), insects are prone to water loss due to their small body size (Tochen et al, 2016). To overcome this limitation, fireflies have behavioral and physiological strategies to avoid water loss. Behaviorally, fireflies avoid water loss by selecting habitats with higher levels of humidity. However, *P. corruscus* was more abundant where the average relative humidity was relatively lower, even though it was still damp (driest site was 79% humidity). The cause of this apparent preference for sites with moderate air humidity remains elusive. One possible explanation is that lower moisture would be less favorable to fungal pathogens (Tochen et al, 2016). Alternatively, this result might be a by-product of this species' adaptations to withstand the relatively drier conditions.

Tree density also explained the presence and abundance of *P. corruscus*, which could be related to pheromone signaling. *Photinus corruscus* have cuticles, also known as the exoskeleton (Drijfhout et al, 2010). The outermost layer of the cuticle consists mostly of hardened proteins, but also has waxes that are referred to as cuticular hydrocarbons [CHC] (Drijfhout et al, 2010). CHC

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are ubiquitous among insects and play a significant role as anti- desiccation agents, preventing water loss, but also aiding in communication (Drijfhout et al, 2010). CHC are secreted from several different glands and accumulate on the outer part of the exoskeleton (South et al, 2008, Ming & Lewis, 2010). With their low volatility, these waxes have been shown to act as contact signals (South et al, 2008, Ming & Lewis, 2010). However, before direct contact can occur, *P. corruscus* must be able to find different aggregations. Like other diurnal fireflies *P. corruscus* females produce volatile sex pheromones that travel throughout the woodlands. Having trees scattered throughout an area versus densely packed perhaps gives a chance of mating opportunities as pheromones could spread more easily to distant colonies of *P. corruscus*.

While the spatial regression revealed humidity and tree density as important components affecting *P. corruscus* abundance across a geographic area, the temporal linear regression revealed air relative humidity, as well as temperature, canopy cover, and leaf litter density affect *P. corruscus* abundance over time. Abundance was highest in the spring months, in areas with temperatures ranging from 17.46C to 11.55C and averaging 14.88C. A preference for colder weather could increase survival rates, as fewer predators are present during the winter months (Deyrup et al, 2017). I also found the highest abundance of fireflies in areas with the most open canopy. While overwintering as adults, *P. corruscus* can typically be found on the south side of the tree where their bodies are wedged into the grooves of the bark (Faust, 2012). While exposing their bodies to the harsh, cold temperatures of winter, being found on the south-facing side of a deciduous tree would allow additional light to reach the bark in the winter, thus providing some warmth to *P. corruscus* individuals. Open canopies allow more light to pass through to the bark and the overwintering fireflies, helping them avoid freezing.

Finally, larvae are influenced by soil moisture and leaf litter density congruency, with soil moisture conceivably providing greater chance of moisture-loving prey, such as snails (Faust, 2017), while the greater leaf litter density likely supplies shelter for the growing coleopteran. I found the greatest abundance of *P. corruscus* in areas with an average leaf litter density of 68.86g, corroborating these hypotheses.

The adjusted R- square value for the temporal regression is smaller compared to the adjusted R- square value for the spatial regression because I collected data for only half the year, from February to August. If this project were replicated with data collected across multiple years rather than six months, it might give a better understanding of the actual temporal variation and more accurate data representing the full lifespan of the firefly.

Clustering and sex ratio in *Photinus corruscus*. My spatial analysis showed that *Photinus corruscus* is highly gregarious in western North Carolina. This gregarious distribution could be the result of males aggregating around females during the breeding season, or both sexes could be aggregating to boost their warning signal to warn off predators, as seen in other firefly species (Faust, 2017; Rooney & Lewis, 2000).

My occurrence data showed that *Photinus corruscus* has a male biased sex ratio in western North Carolina. More males than females can result in greater competition among males, which can affect the trajectory of the populations (Buunk & Fisher, 2009). There are a few reasons for this, one being that the females are not flying around as much as males, leading to a sex-specific dispersal. Such a phenomenon makes sense if females are rarer and get to choose among competing males. This is well-known in fireflies with physogastric or flightless females (Cicero, 1988), and is a common trend in fireflies (South et al, 2008). With females being the choosier sex, the males are the ones doing the seeking out. Although there is no evidence in the literature specifically for

Photiuns corruscus, other reasoning could be female death rates, which could be higher due to disease. There could possibly be a disease that targets the female reproductive system, killing them off one by one.

Conclusion. This study is the first-time environmental variables have been measured for a diurnal firefly, making it a significant contribution to the natural history of fireflies. Further, this research may provide insights into firefly evolutionary history. For instance, by understanding habitat requirements for diurnal fireflies, researchers can determine which environmental factors are important to threatened fireflies. To keep diurnal firefly knowledge growing, others could continue this journey and replicate my methods for other species, as well as continue this study during the winter months for *Photinus corruscus*. Furthermore, it is still unknown whether *P. corruscus,* as currently defined, represents a single or multiple species. By utilizing these results, future researchers can see if patterns of microsatellite or other genetic markers can be linked to certain environmental tolerances to start providing information on the *P. corruscus* species complex. Firefly researchers now have a better idea of what this mysterious species needs for its survival; It is a start, most certainly not the end, to an ongoing study on something we know little about.

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APPENDICES

Table. A1 Raw data of environmental variables associated with Balsam.

Balsam	TEMP	HUMID	LEAFLIDEN	SOILMOIS	THROUGHFALL	CANOPYCOVER	TREEDEN	TREEDIAM	APPTOWATER
3/15/2021	10.55	59.41	55.5	22.78	159	N/A	0.1	23.73	320
3/29/2021	12.22	78.8	70.24	25.59	1,449	23.14	0.1	23.73	320
4/12/2021	11.86	61.3	31.8	22.72	373	9.36	0.1	23.73	320
4/26/2021	11.55	57.32	79.62	22.51	91	15.08	0.1	23.73	320
5/10/2021	15.53	70.29	76.15	23.38	632	9.62	0.1	23.73	320
5/24/2021	14.98	72.74	37.43	N/A	80	5.46	0.1	23.73	320
6/7/2021	17.46	83.31	78.97	N/A	283	3.38	0.1	23.73	320
6/27/2021	18.53	88.53	41.98	22.23	420	2.86	0.1	23.73	320
7/11/2021	18.97	91.48	105.73	16.64	271	2.6	0.1	23.73	320
7/25/2021	19.46	93.74	62.06	14.9	123	4.16	0.1	23.73	320
8/8/2021	19.24	92.74	67.9	22.3	500	2.34	0.1	23.73	320
8/21/2021	19.55	98.57	119.01	27	1278	3.12	0.1	23.73	320
AVERAGE	15.825	79.0192	68.86583333	22.005	471.5833333	7.374545455	0.1	23.73	320

Table. A2 Raw data of environmental variables associated with Tessentee.

Tessentee	TEMP	HUMID	LEAFLIDEN	SOILMOIS	THROUGHFALL	CANOPYCOVER	TREEDEN	TREEDIAM	APPTOWATER
3/15/2021	11.76	62.6	57.31	22.32	0	N/A	0.13	15.23	146.3
3/29/2021	13.87	85.4	95.08	30.03	1,596	30.68	0.13	15.23	146.3
4/12/2021	12.88	69.53	41.08	27	505	14.82	0.13	15.23	146.3
4/26/2021	13.5	66.04	86.17	26.4	61	15.34	0.13	15.23	146.3
5/10/2021	17.7	73.32	65.45	25.5	491	19.24	0.13	15.23	146.3
5/24/2021	17.08	77.52	48.06	N/A	35	13	0.13	15.23	146.3
6/7/2021	19.62	83.19	68.67	N/A	283	5.72	0.13	15.23	146.3
6/26/2021	20.58	90.9	52.62	22.46	635	6.5	0.13	15.23	146.3
7/10/2021	20.94	92.75	94.65	17.36	284	8.06	0.13	15.23	146.3
7/25/2021	21.33	98.22	93.48	21.75	333	6.5	0.13	15.23	146.3
8/7/2021	21.58	93.45	76.58	6.55	81	4.68	0.13	15.23	146.3
8/21/2021	21.88	95.46	136.14	26.94	1,212	5.2	0.13	15.23	146.3
AVERAGE	17.727	82.365	76.27416667	22.631	459.6666667	11.79454545	0.13	15.23	146.3

Table. A3 Raw data of environmental variables associated with Sloan Pond.

Sloan Pond	TEMP	HUMID	LEAFLIDEN	SOILMOIS	THROUGHFALL	CANOPYCOVER	TREEDEN	TREEDIAM
3/16/2021	12.79	48.28	107.37	35.93	278	N/A	0.59	11.44
3/30/2021	14.25	72.58	16.33	29.08	907	30.68	0.59	11.44
4/13/2021	14.04	64.28	17.59	32.55	223	12.74	0.59	11.44
4/27/2021	12.38	66.04	35.12	32.58	70	12.22	0.59	11.44
5/11/2021	15.52	79.63	54.23	33.32	682	8.58	0.59	11.44
5/24/2021	15.29	82.49	29.11	N/A	110	16.38	0.59	11.44
6/7/2021	18.08	86.54	62.19	N/A	317	7.54	0.59	11.44
6/27/2021	19.14	91.99	35.31	30.4	622	6.5	0.59	11.44
7/10/2021	19.66	92.87	64.15	27.05	291	9.36	0.59	11.44
7/24/2021	19.89	97.66	54.26	25.62	261	4.68	0.59	11.44
8/7/2021	19.93	97.11	55.86	41.56	444	4.68	0.59	11.44
8/21/2021	20.06	100.19	133.16	38.4	1,200	5.46	0.59	11.44
AVERAGE	16.753	81.63833	55.39	32.649	450.4166667	10.80181818	0.59	11.44

Table. A4 Raw data of environmental variables associated with Sloan Woods.

Sloan Woods	TEMP	HUMID	LEAFLIDEN	SOILMOIS	THROUGHFALL	CANOPYCOVER	TREEDEN	TREEDIAM	APPTOWATER
3/16/2021	10.34	56.87	68.06	36.43	259	N/A	0.41	3.4	134.14
3/30/2021	12.2	82.8	38.38	30.66	1,230	N/A	0.41	3.4	134.14
4/13/2021	11.83	66.19	22.47	27.79	276	21.58	0.41	3.4	134.14
4/27/2021	11.73	63.37	44.59	28.17	80	8.84	0.41	3.4	134.14
5/11/2021	15.31	78.95	73.93	29.44	619	5.72	0.41	3.4	134.14
5/24/2021	14.92	86.75	65.06	N/A	102	6.76	0.41	3.4	134.14
6/7/2021	17.81	86.92	93.8	N/A	216	5.46	0.41	3.4	134.14
6/27/2021	18.86	93.79	39.63	27	674	3.12	0.41	3.4	134.14
7/10/2021	19.47	94.48	98.38	26.88	320	7.54	0.41	3.4	134.14
7/24/2021	19.72	98.13	90.95	22.08	262	3.9	0.41	3.4	134.14
8/7/2021	19.8	97.43	78.79	37.78	460	3.38	0.41	3.4	134.14
8/21/2021	N/A	N/A	N/A	N/A	N/A	N/A	0.41	3.4	134.14
AVERAGE	15.98166667	83.86666667	73.4675	30.454	455.3333333	6.968	0.41	3.4	134.14

Table. A5 Raw data of environmental variables associated with WCU Trail.

WCU Trail	TEMP	HUMID	LEAFLIDEN	SOILMOIS	THROUGHFALL	CANOPYCOVER	TREEDEN	TREEDIAM	APPTOWATER
3/20/2021	10.42	71.54	31.81	20.15	448	N/A	0.3	9.24	545
3/30/2021	13.26	75.85	19.15	22.75	769	11.18	0.3	9.24	545
4/13/2021	12.88	63	29.21	25.3	217	10.14	0.3	9.24	545
4/27/2021	12.05	61.87	33.56	25.82	91	4.42	0.3	9.24	545
5/13/2021	14.45	82.09	62.79	N/A	716	N/A	0.3	9.24	545
5/24/2021	16.2	77.7	27.89	N/A	0	6.76	0.3	9.24	545
6/7/2021	18.16	85.87	73.03	N/A	74	3.38	0.3	9.24	545
6/27/2021	19.5	90.62	27.59	14.97	693	4.94	0.3	9.24	545
7/11/2021	20.12	91.2	68.04	18.5	302	4.42	0.3	9.24	545
7/24/2021	20.25	97.18	106.43	14.92	771	3.12	0.3	9.24	545
8/8/2021	20.34	95.38	98.59	28.02	839	1.04	0.3	9.24	545
8/21/2021	N/A	N/A	N/A	N/A	N/A	N/A	0.3	9.24	545
AVERAGE	16.53416667	82.51416667	60.46583333	21.93888889	507.9166667	5.226	0.3	9.24	545

Table. A6 Raw data of environmental variables associated with Wolf Creek.

Wolf Creek	TEMP	HUMID	LEAFLIDEN	SOILMOIS	THROUGHFALL	CANOPYCOVER	TREEDEN	TREEDIAM	APPTOWATER
3/15/2021	9.75	54.59	81.62	34.54	122	N/A	0.13	8.13	15.24
3/29/2021	11.92	77.12	27.12	38.18	1,274	21.58	0.13	8.13	15.24
4/12/2021	10.68	64.94	24.75	34.18	451	16.12	0.13	8.13	15.24
4/26/2021	10.73	60.95	69.54	32	141	9.36	0.13	8.13	15.24
5/10/2021	14.48	74.42	58.9	36.09	513	8.84	0.13	8.13	15.24
5/24/2021	14.25	83.52	31.04	N/A	84	7.8	0.13	8.13	15.24
6/7/2021	16.63	89.16	82.52	N/A	400	4.94	0.13	8.13	15.24
6/27/2021	17.94	93.58	45.3	38.5	N/A	4.94	0.13	8.13	15.24
7/11/2021	18.57	95.75	79.54	30.2	N/A	3.64	0.13	8.13	15.24
7/24/2021	19.26	97.67	92.2	24.11	N/A	15.34	0.13	8.13	15.24
8/8/2021	19.61	96.82	82.08	31.73	551	7.8	0.13	8.13	15.24
8/21/2021	N/A	N/A	N/A	N/A	N/A	N/A	0.13	8.13	15.24
AVERAGE	15.28	82.49	62.93	34.38	496	9.8	0.13	8.13	15.24

Table. A7 Raw data of environmental variables associated with High Falls Trail.

Highfalls	TEMP	HUMID	LEAFLIDEN	SOILMOIS	THROUGHFALL	CANOPYCOVER	TREEDEN	TREEDIAM	APPTOWATER
3/16/2021	9.07	67.13	69.68	36.33	420	N/A	0.11	20.16	51.12
3/30/2021	12.36	80.48	27.12	31.33	1,274	15.34	0.11	20.16	51.12
4/13/2021	12.12	70.35	24.38	30.1	416	26.26	0.11	20.16	51.12
4/27/2021	12.39	67.75	32.38	27.01	81	21.06	0.11	20.16	51.12
5/13/2021	14.63	82.45	50.93	N/A	653	N/A	0.11	20.16	51.12
5/25/2021	15.77	85.7	30.91	N/A	0	8.58	0.11	20.16	51.12
6/8/2021	17.26	93.6	100.44	N/A	852	4.16	0.11	20.16	51.12
6/27/2021	18.48	96.31	59.28	34.23	541	5.46	0.11	20.16	51.12
7/11/2021	19.08	96.87	93.97	25.78	317	2.86	0.11	20.16	51.12
7/25/2021	19.39	101.28	87.79	24.66	N/A	3.38	0.11	20.16	51.12
8/8/2021	19.13	99.38	73.65	15.85	386	2.34	0.11	20.16	51.12
8/22/2021	N/A	N/A	N/A	N/A	N/A	N/A	0.11	20.16	51.12
AVERAGE	15.78333333	86.93083333	61.045	28.32111111	559.0909091	9.048	0.11	20.16	51.12

Table. A8 Raw data of environmental variables associated with Laurel Knob.

Laurel Knob	TEMP	HUMID	LEAFLIDEN	SOILMOIS	THROUGHFALL	CANOPYCOVER	TREEDEN	TREEDIAM	APPTOWATER
3/16/2021	10.49	55.24	22.68	41.26	66	N/A	0.13	14.45	860
3/30/2021	11.11	84.98	26.85	36.53	1,542	39.78	0.13	14.45	860
4/13/2021	11.43	65.69	16.7	31.7	705	42.9	0.13	14.45	860
4/27/2021	10.71	64.62	21.95	31.74	263	36.14	0.13	14.45	860
5/13/2021	13.27	78.01	58.6	34.13	630	50.7	0.13	14.45	860
5/25/2021	15.56	75.48	31.7	N/A	0	57.72	0.13	14.45	860
6/8/2021	16.15	88.72	106.78	N/A	689	19.5	0.13	14.45	860
6/27/2021	16.38	97.58	43.17	21.68	789	30.94	0.13	14.45	860
7/11/2021	16.84	101.02	54.13	27.7	425	22.36	0.13	14.45	860
7/25/2021	17.38	101.64	37.59	21.6	386	31.2	0.13	14.45	860
8/8/2021	17.57	98.31	37.38	27.55	971	31.2	0.13	14.45	860
8/22/2021	N/A	N/A	N/A	N/A	N/A	N/A	0.13	14.45	860
AVERAGE	14.57166667	84.29416667	43.0725	31.461	651.0833333	35.57272727	0.13	14.45	860

Table. A9 Raw data of environmental variables associated with Highlands Creek.

Highland Creek	TEMP	HUMID	LEAFLIDEN	SOILMOIS	THROUGHFALL	CANOPYCOVER	TREEDEN	TREEDIAM	APPTOWATER
3/16/2021	7.76	86.37	61	35.97	829	N/A	0.49	12.07	7.62
3/30/2021	10.58	89.16	38.07	32.02	1,581	2.34	0.49	12.07	7.62
4/13/2021	9.34	80.61	27.45	27.5	1,462	0.78	0.49	12.07	7.62
4/27/2021	9.36	75.94	34.23	25.42	371	2.08	0.49	12.07	7.62
5/13/2021	12.21	88.95	78.07	31.75	1,499	4.68	0.49	12.07	7.62
5/25/2021	14.04	88.16	22.76	N/A	0	1.82	0.49	12.07	7.62
6/8/2021	15.82	95.47	127.11	N/A	855	3.12	0.49	12.07	7.62
6/27/2021	16.99	100.1	68.57	37.45	676	1.04	0.49	12.07	7.62
7/11/2021	17.37	102.48	89.19	31.4	347	2.34	0.49	12.07	7.62
8/1/2021	18.46	102.68	75.16	42.5	564	2.34	0.49	12.07	7.62
8/8/2021	16.51	100.82	88.07	38.82	127	1.82	0.49	12.07	7.62
8/22/2021	N/A	N/A	N/A	N/A	N/A	N/A	0.49	12.07	7.62
AVERAGE	13.895	92.40333333	64.30583333	34.485	804.25	2.174545455	0.49	12.07	7.62

Table. A10 Raw data of environmental variables associated with Highlands Woods.

Highland Woods	TEMP	HUMID	LEAFLIDEN	SOILMOIS	THROUGHFALL	CANOPYCOVER	TREEDEN	TREEDIAM	APPTOWATER
3/16/2021	7.22	78.8	116	29.97	877	N/A	0.67	5.55	8.53
3/30/2021	10.13	93.33	54.78	31.07	1,436	2.08	0.67	5.55	8.53
4/13/2021	8.88	84.66	29.19	33.42	694	0.26	0.67	5.55	8.53
4/27/2021	8.86	79.24	52.8	23.07	198	2.34	0.67	5.55	8.53
5/13/2021	11.64	92.11	133.82	35.55	618	2.6	0.67	5.55	8.53
5/25/2021	14.01	88.08	33.88	N/A	0	1.3	0.67	5.55	8.53
6/8/2021	15.77	95.23	118.66	N/A	691	2.6	0.67	5.55	8.53
6/27/2021	16.9	100.38	142.3	29.8	565	1.04	0.67	5.55	8.53
7/11/2021	17.41	101.4	129.16	29.57	347	0.26	0.67	5.55	8.53
8/1/2021	18.41	102.22	89.32	25.87	545	2.08	0.67	5.55	8.53
8/8/2021	16.4	101.54	75.62	26.7	86	0.52	0.67	5.55	8.53
8/22/2021	N/A	N/A	N/A	N/A	N/A	N/A	0.67	5.55	8.53
AVERAGE	13.66083333	93.38916667	87.92416667	29.977	612.3333333	1.465454545	0.67	5.55	8.53

Table. A11 Raw data of environmental variables associated with Satulah.

Satulah	TEMP	HUMID	LEAFLIDEN	SOILMOIS	THROUGHFALL	CANOPYCOVER	TREEDEN	TREEDIAM	APPTOWATER
3/20/2021	N/A	N/A	42.18	34.13	584	N/A	0.4	11.21	776
3/30/2021	10.45	86.07	41.27	32.23	1,557	16.9	0.4	11.21	776
4/13/2021	10.65	70.2	60.76	29.91	1,096	14.82	0.4	11.21	776
4/27/2021	10.37	67.2	70.09	27.05	324	16.12	0.4	11.21	776
5/13/2021	12.24	85.21	64.22	30.46	1,013	22.62	0.4	11.21	776
5/25/2021	15.35	75	33.01	N/A	0	10.92	0.4	11.21	776
6/8/2021	15.99	91.84	125.47	N/A	970	9.88	0.4	11.21	776
6/27/2021	16.71	96.84	94.84	32.6	993	11.7	0.4	11.21	776
7/11/2021	17.27	99.81	93.28	26.46	479	6.76	0.4	11.21	776
7/25/2021	17.63	102.22	85.29	37.16	756	15.6	0.4	11.21	776
8/8/2021	17.86	97.12	51.14	23.53	200	8.84	0.4	11.21	776
8/22/2021	N/A	N/A	N/A	N/A	N/A	N/A	0.4	11.21	776
AVERAGE	14.79909091	88.49909091	70.91083333	30.833	785.1666667	13.21272727	0.4	11.21	776

Table. A12 Raw data of environmental variables associated with Brushy Face.

Brushy Face	TEMP	HUMID	LEAFLIDEN	SOILMOIS	THROUGHFALL	CANOPYCOVER	TREEDEN	TREEDIAM	APPTOWATER
3/20/2021	7.98	79.53	54.37	34.74	879	N/A	0.34	8.71	9.05
3/30/2021	10.58	89.06	29.88	33.26	1,485	10.92	0.34	8.71	9.05
4/13/2021	8.89	81.96	29.03	30.93	1,328	4.16	0.34	8.71	9.05
4/27/2021	8.98	76.27	45.45	31.61	170	4.16	0.34	8.71	9.05
5/13/2021	12.14	89.22	72.9	26.35	1,354	13.26	0.34	8.71	9.05
5/25/2021	27.14	84.8	32.03	N/A	0	2.34	0.34	8.71	9.05
6/8/2021	16.1	94.68	135.23	N/A	497	11.7	0.34	8.71	9.05
6/27/2021	17.18	100.43	115.24	26.77	883	6.76	0.34	8.71	9.05
7/11/2021	17.49	102.88	107.92	27.8	434	4.42	0.34	8.71	9.05
8/1/2021	18.51	104.2	87.66	28.62	559	6.24	0.34	8.71	9.05
8/8/2021	16.64	104.2	80.42	30.6	117	4.94	0.34	8.71	9.05
8/22/2021	N/A	N/A	N/A	N/A	N/A	N/A	0.34	8.71	9.05
AVERAGE	15.005	92.8158	72.9575	30.861	760.1666667	6.665454545	0.34	8.71	9.05