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When the Leaves Fall: Modeling Seasonal Variation of Litter Flux in an Urban Forest

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Modeling seasonal variation of litter flux in an urban forest

An Honors Thesis submitted in partial fulfillment of the requirements for Honors in Biology.

By
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Under the mentorship of Dr. Checo Colón-Gaud

Abstract

I propose a statistical model to describe the seasonal variation in forest litter flux rates. To examine the effectiveness of the proposed model and to estimate the model parameters, a small set of litter flux data was collected. Data collection was continuous from November 2014 to January 2016. Model parameters were estimated from the data. Using the estimated parameters, the model was applied to an existing dataset to provide some evidence of the model's potential to predict future litter flux rates. While the model did reasonably fit the data, it only had some limited success at prediction. Future research is needed to test the model's utility.

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Introduction

Forest litter fall (e.g. leaves, branches, flowers, cones, etc.) represents a flux of carbon, moving sequestered carbon from the forest canopy to the forest floor (Bardgett 2005; De Deyn et al. 2008; Chapin et al. 2011). Decomposition will release much of this carbon back into the atmosphere with a small quantity of recalcitrant carbon compounds remaining in the soil for an indefinite period of time (Bardgett 2005; De Deyn et al. 2008; Chapin et al. 2011). Ecosystem respiration has a greater effect on overall carbon balance within most ecosystems, and soil respiration represents the greatest contribution to total ecosystem respiration (Schlesinger 2000; Chapin et al. 2011). Since litter fall is one of the major carbon input to the soil (Bardgett 2005; Chapin et al. 2011), understanding patterns and cycles in litter flux leads to better inferences about the nature of soil respiration. In most if not all ecosystems, litter flux varies over the seasons as do other ecosystem processes. Leaf litter is the most common form of litter, and thus leaf phenology heavily affects total litter phenology. While seasonal variation in litter flux is self-evident in deciduous forests with large increase in litter flux during the fall months, similar seasonal variation is present in the traditionally *Pinus*-dominant ecosystems of the Southeastern United States.

While studies have been conducted on litter phenology before (Meentemeyer et al. 1982; Melillo et al. 1982; Wang et al. 2013), it seems no study has yet proposed a general mathematical model of the seasonal cycles in litter flux. Such a model could provide valuable insight by quantifying and predicting litter flux throughout the course of a year. An accurate model of seasonal variation could inform other studies of interannual variation by mathematically accounting for seasonal variation. Lastly, as climate change influences patterns in seasonal variation and in interannual variation, an accurate model could provide a historical norm against which future deviations in litter flux may be measured. In this study, I propose a general mathematical model to predict expected litter flux based on the time of year (i.e. the ordinal day of the year). Using experimental data collected in a small urban forest patch in Southeastern Georgia, USA, I estimated relevant model parameters. Finally, I discuss the model's potential and its theoretical limitations in reviewing its effectiveness in describing earlier experimental data.

Methodology

Litter flux was observed on a continuous basis for 432 days beginning on November 13, 2014 until January 19, 2016. This dataset was used to construct a model detailed below. Data collection took place inside a section of Charles H. Herty Pines Nature Preserve ("Herty Pines"). Herty Pines is an urban forest located on the campus of Georgia Southern University in Statesboro, Georgia, USA (32°25'49.68"N, 81°47'2.58"W). The area is surrounded by light or moderately urbanized areas (i.e. urban sprawl) including housing developments, strip malls, university buildings, and athletic complexes and has few natural corridors to other areas. Herty Pines is less than 10 kilometers from downtown Statesboro, well within the city limits[1]. Herty Pines may be divided into two ecologically distinct regions: the Northwest consisting primarily of low lying wetland[2] with few understory tree species (>3 m tall; shorter than canopy individuals) and the Southeast consisting primarily of gently sloped land with many mixed canopy and understory tree species. The Southeast varies from open areas with widely spaced trees to areas of thick underbrush and understory growth. The total difference in height across the site is likely less than 10 meters. Deciduous tree species including magnolia (*Magnolia grandiflora*), water oak (*Quercus nigra*), sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), and a few individuals of dogwood (*Cornus florida*), tulip-popular (*Liriodendron tulipifera*), American holly

[1]Statesboro is a small rural city with a fair number of forest patches, but there is little connection between them due to roads, fields, and building complexes.

[2]Primarily ephemeral standing water with little to no flow across the site. Standing water is greatest during the winter months likely due to a decrease in evapotranspiration as summer precipitation is generally higher than winter precipitation.

(*Ilex opaca*), and sycamore (*Platanus occidentalis*) may be found throughout the site, but tend to dominate the Southeast. Natives pine species such as longleaf pine (*Pinus palustris*), loblolly pine (*Pinus taeda*), and slash pine (*Pinus elliotti*) also may be found throughout the site, but dominate the Northwest portion. This area possesses a wetter topography and thus a canopy that consists almost entirely of the *Pinus* species[3] with deciduous species occurring mainly near the periphery or as sporadic understory trees[4].

All measurements were made in the Northwestern section since this area is ecologically more homogeneous and is closer to the traditional longleaf-wiregrass habitat that once was the main ecosystem of the Southeastern United States Coastal Plains. Management and human traffic was, at the time of this writing, infrequent throughout the site. Currently, the site is slated to be burned every ten years[5] and appears to have been burned most recently in 2010 as the culmination of a project to restore the site to a more natural state prior to European colonization (Bryant 2009; Williams 2011). Although a number of walkways and paths seemed to have been created for use as part of a nature walk, human traffic and maintenance of these paths is limited. A few other projects were in progress on site, but not within measurement areas, and should not have affected the data presented herein.

Twenty-four 0.25 m^2 traps were placed within the Northwest of Herty Pines. Each trap acted as a single replicate of sampling for the entire plot. Although the location of each trap was not randomized, traps were placed in a fashion to approximate a uniform distribution throughout the site while remaining easily accessible to researchers.

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[3] *P. taeda* is thought to dominate among the pines.

[4] I know of no current, exhaustive inventory of species present at Herty Pines. See Drapalik and French (1983) for more information. I have given known canopy species to characterize the site based on personal knowledge. The model I propose will hopefully be applicable to other ecosystems with different species compositions.

[5] An informal conversation with an employee from Georgia Southern University Landscape Services. However, in other informal conversations, members of the Biology Department faculty have claimed that controlled burning of the site is unlikely to occur again due to problems with smoke and fire control.

Table 1: Definitions of Each Category for the Sorting of Sample Contents and Totals

Category	Definition
Needles	Conifer or pine needles
Leaves	Broad leaves of deciduous trees (e.g oak)
Reproductive Structures	Male and female cones, oak flowers, etc.
Wood	Bark or branches (whole branches with leaves or needles also included)
Miscellaneous	Remaining mass, small debris, unknown parts, small amounts (<1 g) of leaves, needles, etc.
Total	Mass of sample and bag − average mass of bag

Litter was collected by hand from traps. Litter samples were dried for a minimum of 1 week[6]. Samples were then individually weighed in grams after which the contents of each sample were sorted (see Table 1 for details) and the sorted contents were individually weighed. Table 1 shows the definitions used to sort the contents of each sample. Samples were discarded after weighing. Sorting allowed for the exploration of seasonal variation among different types of litter. Traps were emptied at varying intervals between 2 and 3 weeks for a total of 19 intervals. All measurements (grams of litter collected in a certain trap during a particular interval) were normalized to grams of litter per meter squared per day ($g \cdot m^{-2} \cdot d^{-1}$).

Modeling Litter Flux

Every trap represents a different sample of litter flux for the study site Herty Pines. At any given point in time, litter flux will vary throughout the site due to several different factors such as the distribution of tree species, micro-climate, and weather

[6]Generally 48-72 hours of drying is sufficient to ensure the removal of all water for the samples. However, the samples must be weighed at 24 hour intervals to track the loss of water and to ensure the total removal of water. To remove these man-hours and conserve time, samples were dried for a week or longer and assumed to be completely dry at the time of processing.

events. Depending on the location of each trap, a different litter flux rate may be observed. This spatial variation in measured litter flux rate likely varies around a mean value which could be used to approximate the total litter flux rate for the entire site. It seems reasonable to assume that the apparently random variation in litter flux may be modeled by a probability distribution such as the normal distribution. Let Λ be the random variable representing this probability distribution, in other words the probability of observing a certain litter flux rate for a given day of the year[7]. If litter flux rates spatially vary according to the normal distribution when aggregated, the measurements presented here would likely fit the Student's t-distribution as a population with unknown parameters (i.e., the entire study site's litter flux rate; averaged per meter squared) was sampled. The following Equation represents a potential model for Λ.

$$\Lambda = \frac{\Gamma\left(\frac{\nu+1}{2}\right)}{\sqrt{\nu\pi}\,\Gamma\left(\frac{\nu}{2}\right)}\left(1+\frac{(\lambda - E(\Lambda))^2}{\nu}\right)^{-\frac{\nu+1}{2}} \tag{1}$$

Λ is the probability of observing a particular value for λ based on ν degrees of freedom[8]. I believe that the expected value of observed litter flux will seasonally vary in a similar fashion from year to year with some deviation due to other variables changing from year to year. Therefore, it seems reasonable to model litter flux seasonal variation as a periodic function, completing a cycle once per year. Trigonometric functions such as sine and cosine are an excellent basis to make models for many periodic relationships. I began model construction with the function described in Equation 2 as a general model form. Let $E(\Lambda)$ be the expected value function of Λ, or the predicted mean value[9]. Note that this mean value is equivalent to $E(\Lambda)$ in

[7]It must be stressed that a random variable is mathematically a function. It is possible to write Λ as $\Lambda(\lambda)$ which is the convention with other functions. Λ is the probability that λ is a certain value or in a certain range. Using the conventions of statistics and probability theory, I omit λ.

[8]$\nu = n - 1$ where n is the number of observations for each interval. Γ is the Gamma Function. $\Gamma(n) = (n-1)!$ for all positive integers n and $\Gamma(t) = \int_0^\infty x^{t-1}e^{-x}\,dx$ for all positive complex numbers t.

[9]For the normal distribution, or the Student's t-distribution, the mean value is also the most

Equation 1.

$$E(\Lambda) = a\cos(\omega t + \phi) + b \tag{2}$$

Where:

$$\begin{aligned}
t &= \text{time (days)} \\
a &= \text{amplitude constant (litter flux; e.g., } \mathrm{g \cdot m^{-2} \cdot d^{-1}}) \\
\omega &= \text{angular frequency constant (radians per day)} \\
\phi &= \text{phase constant (radians)} \\
b &= \text{height constant (litter flux; e.g., } \mathrm{g \cdot m^{-2} \cdot d^{-1}})
\end{aligned}$$

With the exception of t which is the independent variable representing time, a, ω, ϕ, and b are model parameters that must be statistically estimated to provide an accurate model. The amplitude or a controls the change in height of the curve. Geometrically, a is the distance from the curve to its midpoint or average value. In other words, a is the maximum deviation from the average value of litter flux for the year. Angular frequency ω is based on the periodicity of the model. If frequency f is the number of cycles completed during a certain time interval, and if period τ is the time to complete a single cycle, then angular frequency is the proportion of a cycle completed during a certain unit of time where a single cycle is equal to 2 π. Mathematically, ω is equal to 2π divided by the period or multiplied by the frequency.

$$\omega = \frac{2\pi}{\tau} = 2\pi f$$

In this case, seasonal variation is expected to have exactly a period of 1 tropical year since the revolution of the Earth around the sun is responsible for the seasons

likely value, or peak of the "bell curve".

and a tropical year is defined as the period of one revolution around the sun. Using the Julian year[10] defined as 365.25 days, ω must then be equal to $\frac{2\pi}{325.25}$ radians per day, or approximately 0.01720242 radians per day.

$$\omega = \frac{2\pi}{365.25} \approx 0.01720242$$

To synchronize the model with the calendar year such that $t = 0$ is equivalent to January 1st, a non-zero phase constant ϕ shifts the curve horizontally. The height constant b is conceptually the average value of the observed data. Model parameters were numerically estimated using non-linear least mean squares with Gauss-Newton algorithm[11] (Fox and Weisberg 2010).

Combining Equations 1 and 2 produces the following Equation:

$$\Lambda(t) = \frac{\Gamma\left(\frac{\nu+1}{2}\right)}{\sqrt{\nu\pi}\,\Gamma\left(\frac{\nu}{2}\right)} \left(1 + \frac{(\lambda - (a\cos(\omega t + \phi) + b))^2}{\nu}\right)^{-\frac{\nu+1}{2}} \tag{3}$$

This Equation is the probability density function or distribution for any given day of the year t. In other words, given a particular value λ and a particular day of the year, $\Lambda(t)$ returns the probability of observing λ as the mean value of all traps. Using this function, it was possible to create confidence intervals for predictions of future mean litter flux values for Herty Pines based on the data. As the number of observations for each time interval varied, the degrees of freedom ν was calculated from the average number of observations. The standard deviation varied from interval

[10] The actual length of a tropical year is closer 365.2422 days. Through the use of leap years, the Julian and Gregorian calendar have average year lengths of 365.25 and 365.2425 days respectively. Both are slightly longer than the actual tropical year, meaning each calendar are slowly becoming desynchronized with the seasons at a rate of one day in 128 years and one day in 3226 years respectively. For simplicity, I decided to use the Julian year in my calculations which means that the model is also slowly desynchronizing with the seasons. However, this desynchronization is negligible over timescales less than 100 years. It is important to note that I use the Julian year here similar to the use of the Julian Date in astronomy, taking the exact year length to be 325.25 days instead of using leap days once every four years.

[11] The statistical analysis programming language R was used to perform the numerical approximation.

to interval and as a result, the standard error varied as well. An average standard error was used to create the confidence intervals.

After estimating the specific model parameters for the models of each category of litter using the experimental data collected during the current study, the models of needle litter flux and total litter flux were applied to a dataset from an earlier study of litter flux at Herty Pines. This previous study collected data from November 2010 to October 2011 and used a similar methodology as the current study.

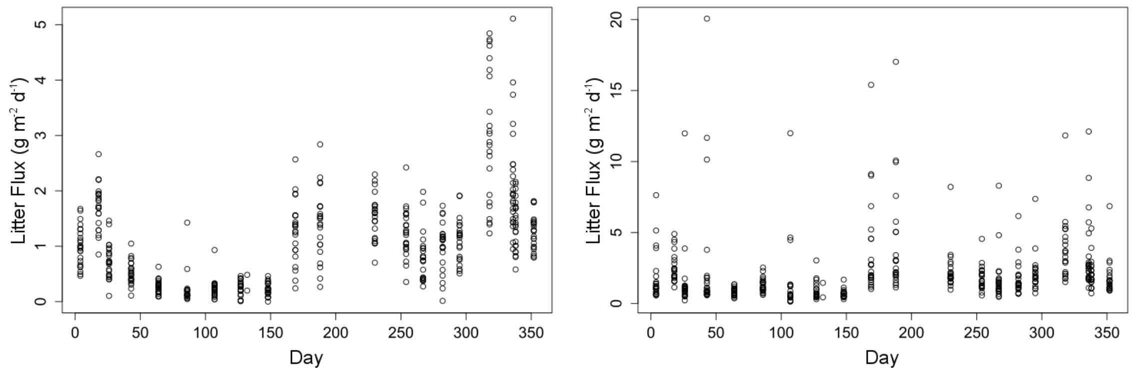
Results

Table 2 compares the total quantity of litter collected during the study period. The majority of litter collected unsurprisingly was pine needles (53%) follow closely by wood (22%). I limit the analysis primarily to the needle litter and total overall litter flux as the other litter categories not only represent small inputs relative to needle litter, but also were more variable both temporally and spatially. No clear seasonal pattern was found in these other litter categories. It is likely that to observe a pattern, if one exists, a larger dataset over longer time scales is needed.

Table 2: Total litter collected in grams per category and as proportion of the total. See Table 1 for category definitions.

Category:	Needles	Leaves	Reprod.	Wood	Misc.	Total
Grams	2838.13	198.17	756.01	1175.59	334.5	5354.9
Proportion	53.00 %	3.70 %	14.12%	21.95%	6.25 %	100.0 %

I believe these types of litter provide the most insight into seasonal variation as other litter flux categories were in small proportions to the needle litter flux. The other litter categories are subsumed in the total litter flux data and have not been totally discarded, but as few useful inferences are possible about the other categories individually, their importance in the analysis and models is reduced. Furthermore, not

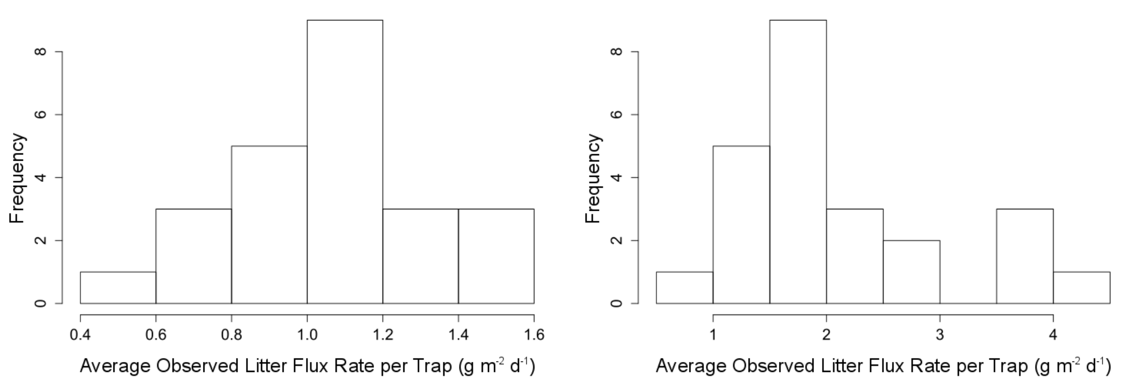


(a) Needle

(b) Total

Figure 1: Plot of observed litter flux in grams per meter squared per day $(\mathrm{g} \cdot \mathrm{m}^{-2} \cdot \mathrm{d}^{-1})$.

enough litter was collected to make any conclusions about the distribution of litter flux rates for other categories. Figure 2 provides some visual evidence of the distribution of needle and total litter flux rates. Comparing the average needle and total litter flux rate from each trap over the entire study period would appear to confirm that the assumption that the spatial variation in litter flux is normally distributed.



(a) Needle

(b) Total

Figure 2: Distribution of average litter flux rates $(\mathrm{g} \cdot \mathrm{m}^{-2} \cdot \mathrm{d}^{-1})$ for the study period.

The assumption that average litter flux rates follow a cosine wave pattern over the course of a year also seems to be valid as shown in Figure 1. Non-linear least mean squares algorithm provided estimates for the parameters of the model (Equation 2). Model parameters[12] are displayed in Table 3 along with 95% confidence intervals ($\alpha = 0.05$) as estimated by the algorithm.

To distinguish the final model form for the pine needle litter flux model from Equations 1 & 2, I denote the expected mean value of needle litter flux as $\eta(t)$ with N representing the probability density function at time t. N returns the probability of observing a mean litter flux rate of n for a particular day t. For the total litter flux model, $\ell(t)$ is the expected mean function and L is probability density function at time t. L returns the probability of observing a mean litter flux rate of l for any given day t. The final model forms are shown below as well as the estimated parameters.

$$\eta(t) = a\cos(\omega t + \phi) + b$$

$$\eta(t) \approx 0.6611\cos(0.0172t + 1.1945) + 1.0098$$

$$N(t) = \frac{\Gamma(11)}{\sqrt{21\pi}\,\Gamma\left(\frac{21}{2}\right)}\left(1 + \frac{(n - \eta(t))^2}{21}\right)^{-11}$$

Note that the functions $N(t)$ and $L(t)$ above and below are identical to Equation 1 with the degree of freedom $\nu = 21$ which was the average of number of observations per interval. Figure 3 plots the models fitted to the experimental data.

$$\ell(t) = a\cos(\omega t + \phi) + b$$

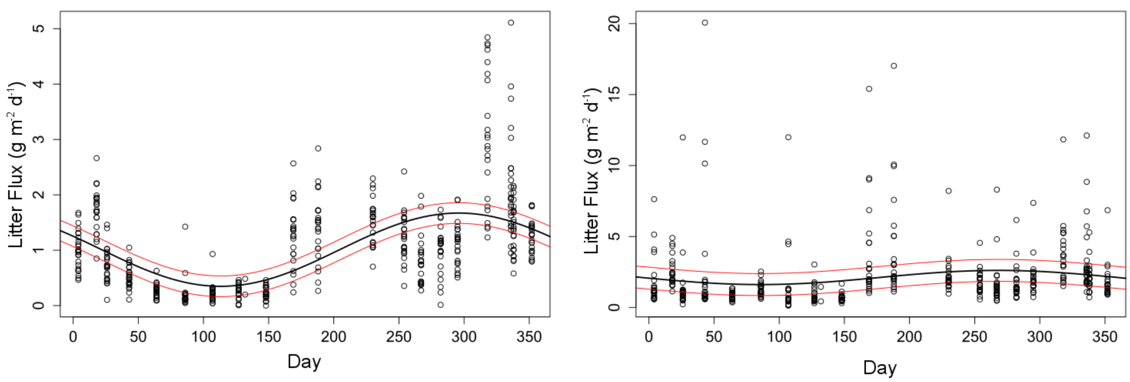
$$\ell(t) \approx 0.4989\cos(0.0172t + 1.6678) + 2.1133$$

$$L(t) = \frac{\Gamma(11)}{\sqrt{21\pi}\,\Gamma\left(\frac{21}{2}\right)}\left(1 + \frac{(l - \ell(t))^2}{21}\right)^{-11}$$

[12] All values are rounded to four decimal places.

Table 3: Estimated constants for daily litter flux rate models for needle litter $\eta(t)$ and total litter $\ell(t)$ with 95% confidence intervals for the b parameter ($\alpha = 0.05$)

Parameters		$\eta(t)$		$\ell(t)$	
a	$\approx$	0.6611		0.4989	
ω	$\approx$	0.0172		0.0172	
ϕ	$\approx$	1.1945		1.6678	
b	$\approx$	1.0098	± 0.1862	2.1133	± 0.7744

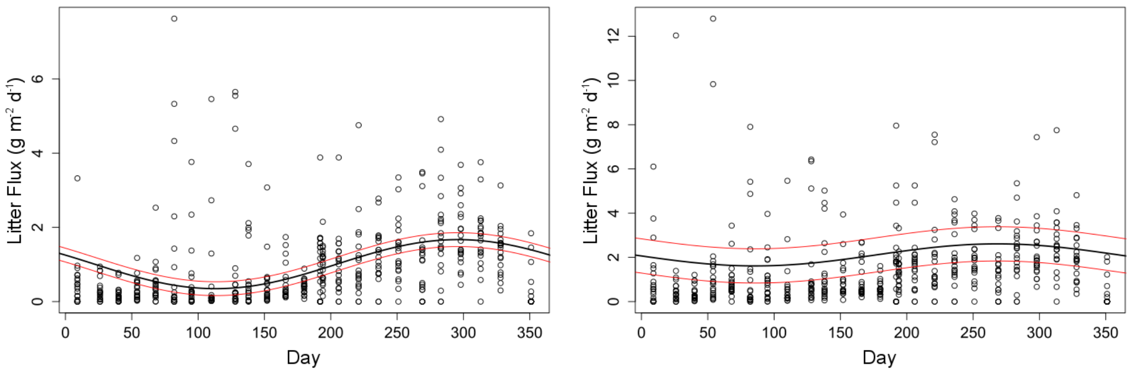


(a) Needle $\eta(t)$ (b) Total $\ell(t)$

Figure 3: $\eta(t)$ and $\ell(t)$ models fitted to the daily litter flux data as a function of ordinal days. Predicted mean in black and 95% confidence intervals in red.

Discussion

Figure 3 shows the proposed model's fit to the experimental data. While the model appears to broadly describe observed seasonal variation in litter flux, some of the datapoints fall outside of the confidence intervals, possibly indicating a weak fit for the model. It may also be that the model underestimates the underlying variability in litter flux due to other variables. The needle litter flux (Figure 3a) especially seems to be highly variable, and much of the late summer observations are spread out far beyond the range of the confidence intervals. However, any true merit of the model is in its potential predictive power. At this time, I cannot make any broad conclusions about the model's predictive power as there has not been any long term studies of



(a) Leaf

(b) Total

Figure 4: Litter flux models $\eta(t)$ and $\ell(t)$ respectively applied to leaf litter flux and total litter flux data from a dataset collected in a similar, earlier study at Herty Pines. The earlier study despite having different experimental parameters observed a similar seasonal pattern as in the current, represented here by the model lines.

the model. Only further research will provide a definitive answer. However, in an attempt to provide a precursory answer, I performed a simple test of the model's predictive accuracy and precision by exploring the model's predictions retroactively.

Using another set of existing experimental data from an earlier study at Herty Pines, I examined the model's performance at describing this second dataset using the model parameters estimated from the current study's data. The methodology used in the earlier study is similar to the current study. Figure 4 shows plots of the model onto the older dataset. The model does not seem to describe any trend in Figure 4 although there does not appear to be the same seasonal variation in litter flux rates. This result may be due to subtle differences in methodology or due to differing environmental conditions. Whatever the case may be, the model performed poorly at describing the earlier dataset suggesting that the model may not perform well at prediction even in more or less the same area. It is also possible that with a dataset spanning several years, the model's predictive power would improve.

Although the model was presented here in the context of describing and predicting litter flux, the model's applications are not limited to litter flux. Indeed, this model

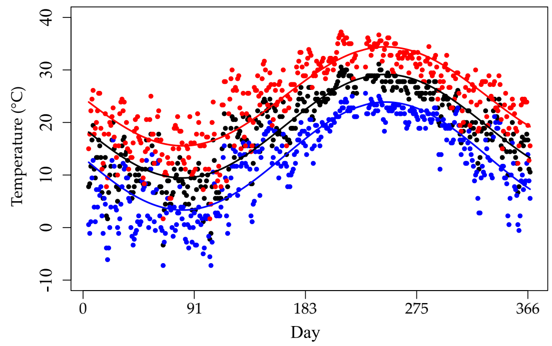


Figure 5: Comparison of daily mean (black), maximum (red), and minimum (blue) temperature models (solid lines) estimated from historical records (2001-2012) to observed temperatures (points) from November 2014 to December 2015 for Statesboro, GA, USA. Day is the ordinal day of the year (e.g., 0 = Jan 1; 364 = Dec 31) with temperatures in degrees Celsius.

may prove better suited to the study of other biological or ecological phenomena, producing more accurate predictions than what was observed here. For example, Figure 5 shows a similar model to Equation 2 predicting the likely mean, maximum, and minimum temperature values for Statesboro, GA along with observed temperature data for a single year. With many years of data, a t-distribution model similar to Equation 1 could be constructed in addition to a simple cosine model. Although climate models far surpass the proposed model, phenomena that vary seasonally or periodically can be modeled statistically using Equation 3. Another example of a potential application might be describing the seasonal variation litter decomposition rates.

As stated in the methodology, climate variables and weather events likely influence the actual litter flux rate. Storms and heavy winds may dramatically increase the amount of litter fall in a short period of time. It is possible that late summer thunderstorms are the primary factor in the increase in litter flux rates in the late summer. Temperature most likely is an important factor as well. However, I am unsure of the exact nature of the relation between temperature and litter flux. No supporting literature on this relationship could be found. Perhaps warmer temperatures correlate with higher litter flux rates by increasing growth rates. Fast growth might lead to a higher turnover rate in leaves (or needles as the case may be) (Chapin et al. 2011). Conversely, perhaps when many trees reduce their growth rates in response to colder temperatures, leaf senescence increases leading to a higher turnover rate in leaves. It is also likely that precipitation and humidity are also an important factor, and are probably closely relatedly to temperature (Vitousek 1984). The lack of similar models and studies make comparisons with existing knowledge difficult.

Modeling these variables may allow for the creation of more accurate models of litter flux. The model proposed here is a simple statistical model. The Equation 1 quantifies the uncertainty inherent in this statistical model giving the model a margin of error. When using the model with confidence intervals, it is important to remember that a 95% confidence level represents a range in which 95% of sample means will be observed assuming the model is accurate. Even if the model is accurately predicting the average litter flux rate, 5% of sample means will still fall outside this range. The breadth of the range describes both the possible variation in litter flux and the precision of the model[13].

Despite this model's potential, it has a few limitations. First, it is dependent on good statistical data of litter flux or of any other variable under study. The experimental data presented here only includes a single year. Ideally, multiple years of data are needed for the best results for any such statistical model. Secondly, this model assumes that litter flux is normally distributed, or that variables other than the day of the year roughly vary according to a normal distribution. Thirdly, this model was built under specific ecological conditions that likely does not hold for other ecosystems. It is possible that the model once fitted to data from a particular area is quite effective at producing statistically accurate predictions[14], but is not accurate

[13] A large degree of precision may still inaccurately predict future litter flux rates.

[14] Statistically accurate predictions being defined as predictions that prove true on average in

when applied elsewhere or when scaling to larger, more heterogeneous ecosystems.

With these limitations in mind, further research could answer some of the remaining questions raised here. I do not expect that all of the assumptions made in the construction of this model will be valid in all situations. I believe that the model may prove effective in understanding many periodic relationships present in the natural world.

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the long run. A correct prediction may yet be too imprecise have much use. As an analogy, an almanach predicts the likelihood of rain on a given day based on past statistics, but a meteorologist may give a more accurate prediction using more sophisticated methods. This model is analogous to the almanach.

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