Bioturbation by mammals and fire interact to alter ecosystem-level nutrient dynamics in longleaf pine forests

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BACKGROUND OF THE STUDY

Bioturbation is the disturbance of sedimentary deposits in soil by living organisms. Actions like burrowing, foraging, ingesting, defecation of sediment grains are all considered as a part of bioturbation. Bioturbation is one of the major forms in which ecosystem engineering takes place. Ecosystem engineers control and affect the rates of nutrient cycling and productivity and contribute to ecosystem functioning and restoration in cases of forest fires, flooding et cetera. Bioturbation helps to redistribute the organic matter and nutrients within the soil. Burial of plant litter and waste products is also a common bioturbation process that alters the rate of decomposition and nutrient cycling. Research has shown that in fire-prone areas, the burial of litter reduces the amount for consumption during fires and alters the distribution of nutrient-rich soil so that a major part of it isn't consumed during forest fires. Additionally, the numbers of vertebrate ecosystem engineers are decreasing and their functions in the ecosystem are being lost before one can fully understand.

This study focuses on bioturbation in longleaf pine forest (*Pinus palustris* Mill.), a fire-adapted ecosystem in southeastern USA. Many ecosystem engineers like southeastern pocket gophers, burrowing beetles, gopher tortoises exist in this ecosystem. Pocket gophers are responsible for the majority of the bioturbation in the forest by forming surface mounds that bury litter, which covers 4% or greater of the forest floor. Due to humans encroaching on this land, naturally ignited fires have been replaced by prescribed burning. Low-intensity fires that occur in 1-5 year intervals are required for maintenance to resemble the historic conditions, but results in depletion of Nitrogen (N) and Phosphorus (P) from the forest floor. Efforts have been made to restore the longleaf pine forest, but ecosystem engineers are desirable as it is a natural process of restoration. Additionally, some of the important ecosystem engineers like southeastern pocket gophers and gopher tortoises are on the decline. Hence, what needs to be analyzed carefully is how bioturbation strengthens the ecosystem functioning of longleaf pine forests.

The researchers formulated a hypothesis that mound-building and interaction of these mounds with fires accelerates decomposition and nutrient turnover and decreases loss of nitrogen and phosphorus. The southeastern pocket gopher was taken as the bioturbator of interest. To study this relationship, the researchers quantified the burial of the litter layer by pocket gophers and measured the nitrogen and phosphorus decomposition rates as well. They also simulated the effect of low-intensity fires to estimate litter consumption and nutrient concentrations. To collect data for the simulation studies, they conducted field censuses to quantify rates of mound formation of pocket gophers; measured the litterfall mass and nitrogen and phosphorus in litterfall over four years in longleaf pine needles and turkey oak (*Quercus laevis* Walt.) foliage. They explored two main ideas which they later evaluated with previously published studies:

1). Effects of pocket gopher mound formation on the ecosystem in terms of litter layer dynamics.

2). Interplay between mound formation rate and fire return interval on nitrogen and phosphorus dynamics.

DATA STRUCTURE

All data used for this project was stored in csv files that were acquired from the Dryad Digital Repository. One csv file was used for plotting both the figures in this project that provided an overview of the litterbag study and is labelled “Mass Nitrogen and Phosphorus in Litterbags Clark et al PLOS ONE”. Values in this table are percent mass remaining, percent nitrogen mass remaining, and percent phosphorus mass remaining in litter in litterbags on the surface of the litter layer or buried beneath pocket gopher mounds after 6, 12, 18, 24, 36 and 48 months. Litterbags initially contained 5.0 grams of turkey oak foliage (Oak), 5.0 grams of longleaf pine needles (Pine), or 2.5 grams of each (Mixed). Data column definitions are:

Litter type = Type of litter in litterbag; Turkey oak, longleaf pine, or mixed.
Block = 1 km2 forest block at the Ordway Swisher Biological Reserve; A, B, C.
Plot = 0.5 ha forest plot within each 1 km2 block; 1 to 12.
Position = Location of litterbag; Surface of litter layer or Buried beneath a pocket gopher mound.
Month = Number of months in the field before harvest.
Percent mass remaining = (Final mass / initial mass) * 100
Percent N mass remaining = (Final nitrogen mass / initial nitrogen mass) * 100
Percent P mass remaining = (Final phosphorus mass / initial phosphorus mass) * 100

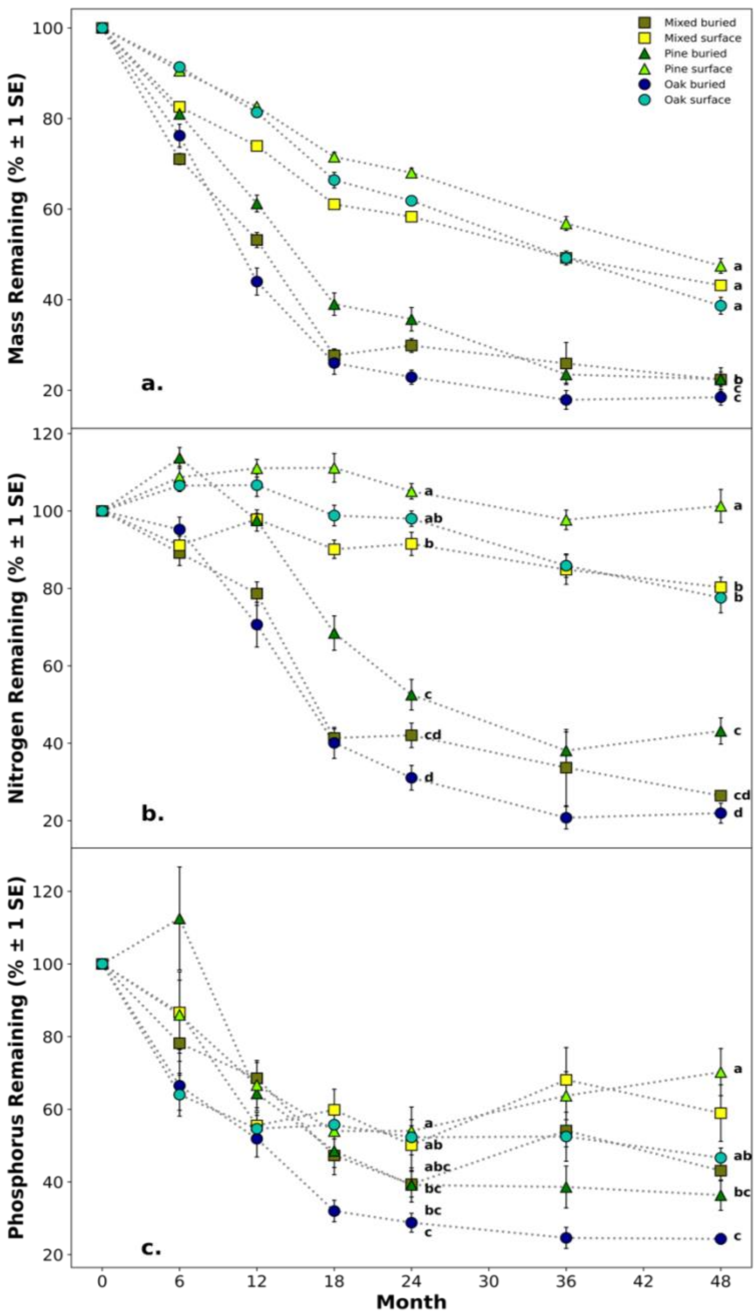
The csv file described above has been split into 3 csv files for ease of access. The data for decomposition of percent mass remaining, percent N mass remaining and percent P mass remaining are found in different files (as the data collected for different plots, positions and time points are not uniform across these measurements) and are stored under "biomass", "nitrogen" and "phosphorus" respectively.

DATA ANALYSIS

Fig 3 deals with mass decomposition, nitrogen and phosphorus dynamics of longleaf pine needle litter, turkey oak litter, and mixed pine and oak litter in litterbags on the surface of the forest floor and buried beneath pocket gopher mounds for four years. Based on these combinations, we have six categories to look into. Each subplot follows the same steps more or less and the basic structure for plotting Fig 3 is outlined below. Let us outline the procedure for the first subplot. Initially, let us input the "biomass" csv file as a dataframe and drop the NaN rows. Then we split the data using pandas groupby function based on columns 'Litter type', 'Position' and 'Months'. Iterating through these separate dataframes, we create a dictionary "std_dict" to store the tuple consisting of 'Litter type', 'Position' and 'Month' as the key and the value would be stored as the tuple consisting of the mean and the standard error of the mean (sem) calculated for the specific dataframe using the scipy.stats library. The figure size and the subplot order are defined. The respective markers, their colors and labels for each category are also defined. X-axis and Y-axis ticks are set so it is uniform across all subplots. The X-axis are the timepoints and the Y-axis is the % of Mass/N/P remaining including the sem error. We initially set a variable 'i' as 0. This acts as a counter and helps us to plot the percent as 100 at time t=0 for every category. Since the std_dict contains every category and six time points spanning 4 years, we check for the remainder of 0 when i is divided by 6 and plot the percent at time t=0 for each category. We iterate through the std_dict dictionary and plot the marker as the mean of the sample considered for every category at each time point and the sem is also denoted as error bars where the vertical width denotes the magnitude of the error. While iterating through the std_dict dictionary, we also append to an empty dictionary called "data_points" that stores the category as the key and the values as a list containing all the means at each timepoint. This data_points dictionary helps to store all the marker positions in a list for each category which helps us to plot a dotted line that connects every category across timepoint. Since the legend across different subplots is the same, we will represent it in the first subplot. We define the marker shape, color and labels and plot the legend in the upper right position of the subplot. We also annotate next to specific litter types and locations that are significantly different ($p < 0.05$) with different letters based on Table 2 in the article. Table 2 contains all the statistics for the significance levels for percent mass remaining that was calculated based on models for decomposition coefficients, k, and the results of the analyses calculated for sets of litterbags in each 0.5 ha plot at the timepoints of 24 and 48 months. This was the basic outline of plotting a subplot in Fig 3 and the same process can be repeated for the other two subplots, taking the 'nitrogen' and 'phosphorus' csv file as an input for the second and the third subplot respectively. One important point to be considered is that file defining the ax for all three subplots should be different and should also contain the gridspec 'gs' order and have the 'shareax' parameter that enables the same X-axis for all subplots.

Fig 4 deals with the relationship between cumulative mass loss and nitrogen concentration in litter in litterbags on the surface of the forest floor and buried beneath pocket gopher mounds over four year**s** a) longleaf pine litter, b) turkey oak litter, c) mixed pine and oak litter**.** Let us initially start with importing the biomass and nitrogen csv and read it as a dataframe. We drop the NaN values. Let us input the initial concentrations of Nitrogen mg of N/ g of litter. The mean value for pine = 3.6, oak = 7.2 and mixed = 5.4. The initial mass of litter is taken as 5g. All of these numbers are present in the article. The total concentration of Nitrogen in terms of mg in each litter type would be the initial mass x initial concentration of N at time t=0. To calculate the X-axis, the cumulative mass loss % is calculated as 100 - 'Percent Mass remaining' in the mass dataframe. To calculate the mass remaining in terms of g = initial mass (which is 5g) x 'Percent Mass remaining'/100. The Y-axis contains the percent of Nitrogen concentration. To calculate these values, let us split the nitrogen and biomass dataframes using the pandas.groupby function and split it based on the Litter type. The split dataframes were named based on their litter type. For us to calculate the mass of nitrogen across each litter type, block, plot, position and month; we create a new column in the dataframe of each litter type called 'Conc of N'= total conc of N at t=0 x 'Percent N mass remaining'/100. To calculate the % of N concentration which is to be plotted on the Y-axis for each litter type, we can create another column in the dataframe for each litter type named '%N conc'= ('Conc of N'x100)/('Mass remaining' x 1000) (We multiply the 'Mass remaining' by 1000 in the denominator to convert g to mg). We then split the litter type based on their position, either buried under pocket gopher mounds or on the surface of the forest floor for the mass and the nitrogen data. Therefore, we end up with 12 dataframes in total that would be utilised for plotting. So, having finished generating the data, we can move on to the regression part and plot the subplots. Since the same template would be followed for all litter types, we can focus on the general outline followed which can be utilised for all. To perform simple linear regression for a category, we need to prepare the X (independent variable) data and y (dependent variable). We then split the X and y data into training and testing sets based on a percentage. We create a LinearRegression object and fit the X and y training data so the model can learn. We then test the model by using the predict function on the object and passing the X test dataset to see how similar the y prediction and y test dataset are. We can then obtain the intercept, coefficient and the r2 score (coefficient of determination) regression **score** function and store all these values in a dictionary that contains all the regression stats. To perform plotting, we set up the GridSpec function to generate 3 subplots where each subplot contains a specific litter type. The axis for a specific subplot is defined with the sharex and sharey parameters so the X and Y axis are the same across all subplots. A scatter plot of each position of litter type is plotted following the same scheme of notation as followed in Fig3. To plot the regression lines, solid lines denote the "surface" position and the dotted line denote the "buried" position, which follows the equation y = slope calculated through regression x dataset X + intercept calculated through regression. The legend is created for all subplots which contain the r2 score next to the label of the marker. This process is repeated for all the remaining litter types and the space between the subplots is adjusted to 0 to represent the paper's plots.

RESULTS AND INTERPRETATION



By looking at the overall figure 3, Mass loss was greater, and N and P were released more rapidly from pine, oak and mixed litter buried beneath pocket gopher mounds than from litter on the surface of the forest floor. Mass loss was initially more rapid from oak and mixed litter (which have a similar distribution) than from pine litter beneath pocket gopher mounds.

Pine and oak litter on the surface initially immobilized N but mixed litter did not. Oak and mixed litter then released N more rapidly than pine litter in both locations. Oak litter that was buried rapidly released N as compared to any other litter type, followed by mixed and pine buried litter. We see an initial increase in N in the surface litter of all categories which reduces over time, the highest increase being pine litter.

Phosphorous also was released more rapidly from buried pine, oak and mixed litter compared to litter on the surface of the forest floor. The amount of P remaining in the mixed litter was intermediate between amounts in pine and oak litter in both locations during most sampling periods. We see the highest increase in P in pine litter buried, which is then the category that contains the lowest P content. Pine surface litter gradually increases and as the highest P content at the end of 4 years. Oak buried litter has the lowest mass, N and P content in terms of % remaining at the end of 4 years.

Litter types and locations that are significantly different ($p < 0.05$) have different letters. Complete statistics are present in Table 2 of the article that reports the different significance levels.

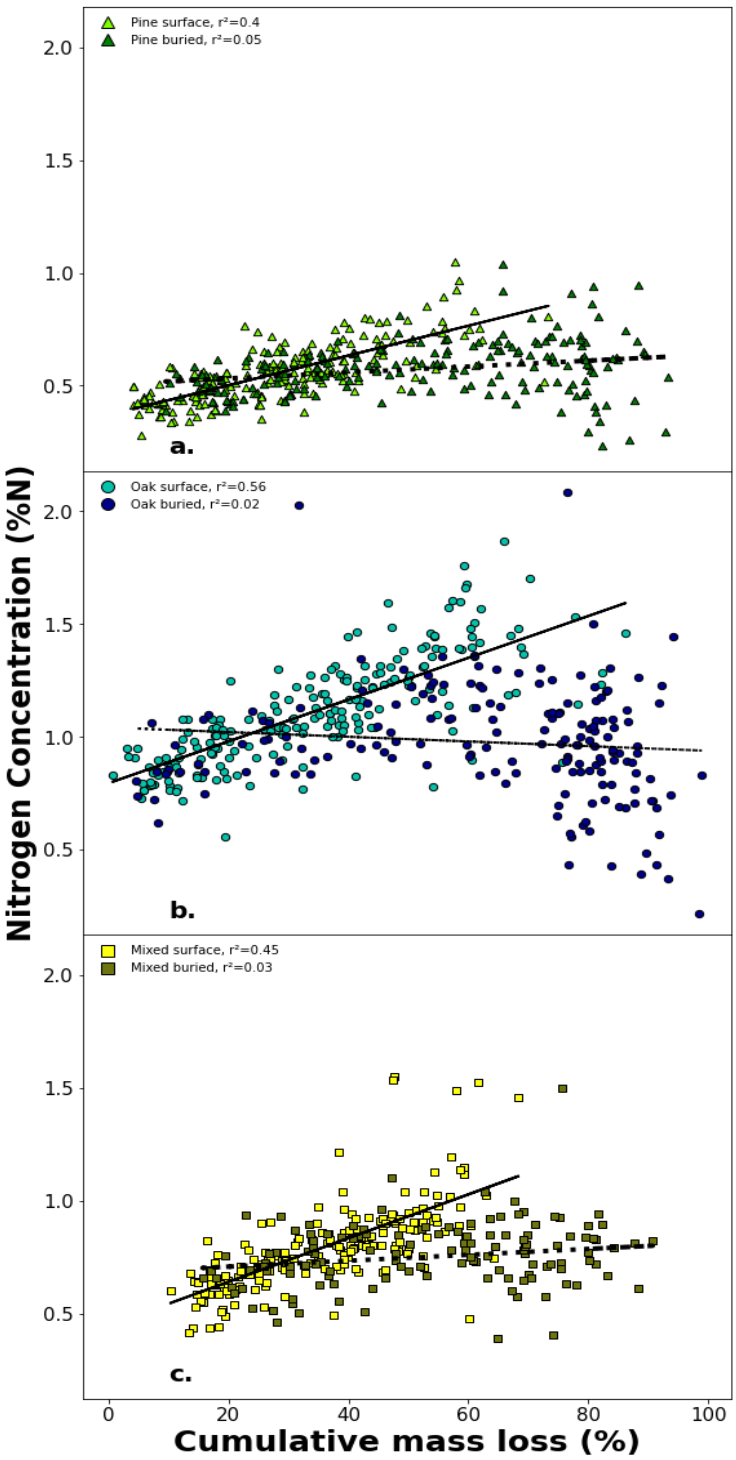


Figure 4 describes the relationship between cumulative mass loss and nitrogen concentration in litter in litterbags on the surface of the forest floor and buried beneath pocket gopher mounds over four years for all litter types. Accumulated mass loss and N concentration were positively related in litter for pine, oak and mixed litter on the surface of the forest floor, but not for buried pine, oak or mixed litter.

r2 or the coefficient of determination is an important metric that helps us to evaluate the performance of a linear regression model. It is the amount of the variation in the output dependent attribute which is predictable from the input independent variable(s). From the figure, r2 is in the order of 0.4-0.5 for surface litter types and almost 0 for the buried litter types. The r2 score is similar to the scores present in the paper but not the same as different libraries were used to calculate these scores.

What we can infer from both of these figures is that the burial of the forest floor by pocket gophers increases the rates of litter decomposition and nutrient turnover, creating patches of enhanced nutrient supply. Vascular plants respond with increased growth of fine roots into buried litter. When forest fires occur, burial of litter is protected from consumption which reduces N and P volatilization. Mass loss from buried plant litter when compared to surface plant litter is more favorable for microbial activity, as it can buffer temperature and moisture content. Burial also facilitates root ingrowth and mycorrhizal colonization in buried litter as decomposition progresses. This study reported that net immobilization of N by buried oak or mixed litter was minimal, and net N release from buried pine and oak litter began relatively early in the decomposition process.

Overall, N and P dynamics in decomposing litter on the surface of the forest floor in our study were similar to other pine-dominated forests in the southeastern US, but N and P were released more rapidly from litter buried beneath pocket gopher mounds compared to unburied litter in other studies.

REFERENCES

Clark, K.L., Branch, L.C. and Farrington, J., 2018. Bioturbation by mammals and fire interact to alter ecosystem-level nutrient dynamics in longleaf pine forests. *PloS one*, *13*(8), p.e0201137.
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