

Response to reviewers

Reviewer response follows copied comments in bold. Responses need to be copied and pasted into the Frontiers forum.

Editor

The authors want to test the hypothesis that differences that might exist due to elevation, that is, between lowlands and highlands, that are more amenable for persistence (high growth capacity, high water use efficiency, etc.) should be erased by fire, and thus, differences between elevations should disappear. To test this, the authors measured several tree and stand variable (height of plants, DBH, tree density, crown area) and leaf D13C, D15N, C, N, P, other macro and micronutrients in the leaf, macronutrients in the soil as well as other water related characteristics. Further, they selected four areas, two in lowlands and two in uplands. Furthermore, at each of the low and highlands they had areas that burned 73 years earlier. The origin of the unburned stands was not provided. Neither was provided the previous fire history of all stands. At each site, they sampled 15 trees or locals for leaf and soil analysis.

First, the origin and fire history at all four sites need to be known in advance, an information that has not been provided.

We have clarified that the other stands had not been burned in the previous 100 years. Although the exact date of the last instance of fire is known in some places throughout Mt. Desert Island, this information was not available at the sites we sampled. All soils were visually inspected for charcoal presence and none was found at any site.

Second, this is a limited experiment, with just one single fire, to test selection by fire without providing the characteristics of fire at two sites (were they high severity fires? Were there surviving trees in the vicinity that could have provided seeds? Were all trees of even age? The authors attempt to indirectly test selectivity by fire on not-first-order fire trait variables, as would have been bark thickness or serotiny. How were the stands regarding these? Moreover, the relationship between these variables and those measured was not clear. The framing of the hypothesis is poorly developed.

We have revised the Introduction to better lay out the study system, clarifying what is and what is not known about the system. We also discuss limitations of unknown factors in the Discussion. With this purely observational, non-manipulative study it was not possible to control for all factors. Despite these limitations, we feel our findings exhibit interesting patterns of plant form and function that result from fire history and topography in the system.

If elevation is such an important factor, the way the trees were selected added a lot of noise. Elevation at which trees were sampled was not homogeneous within sites, with differences of over 200 m. So, elevation was not a qualitative factor but a quantitative one that should have been dealt with as a covariate, rather than a categorical variable. Additionally, there were variations in aspect, which, as confirmed in the analysis, should have been included in the statistical models as a covariate. More to, the sites were also probably different in terms of soil depth, although much information was not provided. It is conceivable that ledges and cliffs support a less deep soil than lowlands. So, elevation has additional covariates that were not accounted for. These are major shortcomings in the design that need to be accounted for before further consideration of the effects of other factors.

I found that the degrees of freedom in the error term of the two-way ANOVA of various models changed from one variable to another. If $n=15$ (number of trees or locations around the trees), it is unclear how such variability in df emerged.

We thank the reviewer for the comments about the statistical analyses. In response, we have revised our statistical analyses in response. Notably, we have included elevation as a continuous factor in our models and have presented the data in the figures along a continuous elevational gradient. We have chosen to include just elevation in our models due to the covariation between elevation and other topographical factors and the inability to include a circular variable (aspect) as predictors in our models. Nonetheless, we have analyzed these factors as dependent variables and discuss their potential impact on soil, leaf, and plant traits in the Discussion. In our linear models, we now use a Type II F-tests to deal with unbalanced data. We have also added text to the “Study sites” section of the methods to clarify the reason for the unbalanced design.

The text is poorly written, with the introduction missing the opportunity to set the scene and objectives of the paper in regard to how fire may have affected the variables measured depending on elevation, and how elevation (and the other covariates) would have also affected tree and stand response. The hypotheses are not clearly stated, and neither are the outcomes expected. The characteristics of the stands are not provided in the methods section. Unclear is also how many samples of leaf tissue were taken and how they were handled lately to obtain a single (?) measure per tree or locals around the trees. That also applies to soil samples. The captions of the results section are sometimes misleading (e.g., D13C when both D13C and D15N are provided; foliar macronutrients, when in fact macro and micronutrients were provided. I missed a global analysis of the various data (e.g., ordination) to better show how the various sites aligned with the hypothesis. Although the authors did not state it, here the main issue of the analysis should have been to find significant interactions documenting the erasing impact of fire, but there were very few such interactions. Greater explanations are needed to justify the results and agreement with the hypothesis.

Thank you for the comments about hypothesis set up and manuscript structure. In response, we have restructured the Introduction to better set up our hypotheses. The hypotheses have also been rewritten to state the expectations more clearly for the measured variables across our observational gradient. The structure of the Methods, Results, and Discussion were also construed to match that set up by the hypotheses. Specifically, in each section we discuss in order topographical features, soil characteristics, leaf traits, and plant-level traits. We hope that this provides better continuity among sections within the manuscript.

In summary, the paper needs a major rewrite and reanalysis. The new version should more clearly state what is the hypothesis that is being tested and develop more explicitly the basis upon which it is constructed, and the outcomes anticipated. In doing so, the authors should consider the limited extent of their experiment given that they have worked with only one fire. Much greater detail about the fire and fire history of the stands needs to be provided. The authors need to justify why they are using an unreplicated study. The new text should address all concerns made by the reviewers. In particular, the points raised by reviewer I about the mechanism by which the expected changes should have occurred need to be fully considered.

Comments to all other reviewer concerns are included in the reviewer forum. All revised portions of the manuscript are marked in red text in the revised manuscript.

Reviewer 1

My only concern about this manuscript is about the introduction section. The authors need to introduce their overview of the topic, their main points of information, and why this subject is important to the scientific world. The authors should introduce the current understanding and background information about the topic. Toward the end of the introduction, the author should

explain how they will provide information to support their research questions. This provides the purpose, focus, and structure for the rest of the paper. As an example, the authors hypothesized greater pitch pine growth and population expansion at low elevation sites as compared to high elevation sites. But why? which is the information behind this? Elevation influence should be first introduced along the introduction section.

Thank you for this comment. We have rewritten parts of the Introduction in response. We now provide support for research questions, and a more thorough explanation of the expected influence of topography on the measured variables as well as their potential interaction with fire. As part of this, we have rewritten the hypothesis section within the Introduction to state these expectations more explicitly.

All revised portions of the manuscript are marked in red text in the revised manuscript.

Reviewer 2

In general, the conceptual model and results were both interesting in isolation. However, I do not believe the results actually align to test the model the authors present in the introduction.

The conceptual model as described in the abstract and intro would suggest that in the absence of fire, pitch pine would shift their resources away from producing traits that help them perpetuate their population after fire, toward traits that allow them to either compete better where environmental conditions are gentle or toward traits that help them tolerate stress. It is not described clearly whether the authors expect this to occur through plasticity of individual trees or through selection over multiple generations. Given the short time window and long life of trees, I suspect plasticity of traits. However, the paper only really measures one trait; WUE. Stand density and tree size could be traits, if stand age was controlled for. However, in this case, stand age was not accounted for. Thus, it is not surprising that the trees that burned in 1947 at higher elevations were shorter than trees at lower elevation that did not burn. They are younger! A really key trait to know about in the testing of this framework would be whether the trees stopped producing serotinous cones in the absence of fire. But this was not reported. I think the study design is inadequate to test the hypothesis. But the results are very interesting and would encourage the authors to focus on presenting just the empirical information they collected.

If the authors choose to keep the conceptual model, I'd urge them to specify more clearly what the recovery persistence traits of pitch pine are? And whether/how it has been shown that those traits relate to slower growth? It would be good to more clearly link the hypothesis in lines 149-158 with the posited qualitative model so that it flows from model right to expectations. What would you expect if the persistence capacity was more prevalent and what would you expect if the recovery capacity was more prevalent? Note, I did not say selection here because that term infers evolutionary processes that take centuries to play out in long-lived organisms like trees.

We thank the reviewer for their comments about the setup of the study. We have dispensed with the use of the resistance/recovery model and have simplified and streamlined the manuscript Introduction to specifically discuss the measured variables, the reason for measuring them, and expected responses. In the Introduction, we couch this within a review of fire history, adaptive characteristics, and the ongoing disappearance of these characteristics (e.g., serotiny). While we agree that measuring other traits would have been interesting and provide an even more comprehensive story, we nonetheless feel that the traits and environmental characteristics we measured here provide a compelling overview of pitch pine strategies across the gradient, while setting the stage for future investigations into other important traits. While, for example, we did not measure age of trees either through cores or a limb method, we did find reasonable evidence of trends in height, canopy and DBH to assign comparative value, and from there to qualify individual stands as tied to one or another of various environmental pressures. Helpfully, we were able to depend on the few reports of ecophysiology, for example, for a portion of the study trees, using

data and observations from previous studies, to firm up an understanding of trends in population demographics, depending in part on a host of factors.

The results should be rearranged and constrained. As it is written, it is not clear why the soil nutrient and water retention data were included. It would be helpful to organize the results so you characterize differences in site conditions and then characterize differences in the pitch pine stands. Shape the results so they directly align and inform your proposed model and expectations if you choose to keep it. As of now, the linkages between model/expectations and results are not clear. Further, there seems to be a mismatch between the presented results and their interpretation. As far as I can tell, there were clear differences in stands due to fire history (described in lines 250-256) but the abstract and discussion both say that elevation was of dominant importance and that fire was less meaningful. But the results as they are described just do not align with this interpretation!

We thank the reviewer for the comment on the structure of the Results, and manuscript in general. In response, we have restructured the Introduction to better set up our hypotheses, including removing the conceptual model. The hypotheses have also been restructured to state the expectations more clearly for the measured variables across our observational gradient. The structure of the Methods, Results, and Discussion were also restructured to match that set up by the hypotheses. Specifically, in each section we discuss in order topographical features, soil characteristics, leaf traits, and plant-level traits. We hope that this provides better continuity among sections within the manuscript.

Line 224-225: Do you mean simple linear model or multiple linear model?

Lines 246-248: Is this a necessary test? How does it influence your conclusions?

Lines 254-255: If the statistical test was insignificant you cannot interpret the difference (because statistically they were not different).

Lines 266-269: Same as previous comment.

Line 272: The relationships you present are correlative not causative since they come from statistics. Consider revising to soil calcium declined with increasing elevation.

Line 273: I am confused about how the linear model could say an effect was significant when the Tukey's did not? This came up for CEC also.

Line 304-306: This interpretation does not align with my understanding of the results. Stand characteristics varied with both fire and elevation. As it was written, it is not clear that one dominated over the other.

Line 326-328: I'm confused. Did the trees measured not produce serotinous cones? Was this measured?

Line 348-352: What does this refer to?

Line 385-388: I'm not familiar with the term ecoservices. I've heard of ecosystem services but that doesn't fit.

Line 393-394: What is an adaptivity curve? The term has not been defined.

Line 403-405: It does not strike me as expansion when one stand is more dense than the other. Expansion is a term used to describe when a tree invades a meadow. But density of an existing stand is a characteristic of successional stage and environmental conditions.

Line 406: But serotiny wasn't measured!

Line 406-407: What does it mean for a tree to exhibit greater buoyancy?

Figures: Too many. Condense and decide which ones strengthen

We have clarified that we used a linear model with three independent factors. As mentioned in the comments to the editor we have restructured our analyses to include elevation as a continuous variable. This excellent suggestion allowed for more simple analyses and easier interpretation of the results. No non-significant results are discussed as having an effect in the Results. We have revised our word to remove any implications of causation. There are no longer contradictions between Anova and Tukeys

results. We did not measure cone serotiny and have removed any implication of such. We have removed the term ecoservices. We have removed the reference to the adaptivity curve. We have replaced the term “expansion” to instead talk about density, the measured variable. We have removed text about buoyancy. We have restructured the figures to show continuous responses. We note that there are still a large number of figures, but have chosen to keep these to illustrate each of the measured variables.