

## **Suggestions for revising manuscripts in response to referee comments.**

Matt Ayres, 29 Aug 2006 (13 Jan 2008, 27 Sept 2017)

Revising manuscripts in response to referee critiques is an important part of the process that seldom gets taught. As an editor, I have seen numerous cases of poor tactics, weak arguments, and inexplicable stubbornness, even from experienced scientists. Following are a few general suggestions and then samples of a few recent revisions from my lab.

My general suggestions for ms revisions are as follows. Whenever possible, respond with "agreed" and just do it. Editors like to see that. On the other hand, one does not want to change the paper too much, and one does not want to accept changes that unnecessarily cripple the message of the paper. When we need to hold our ground on something, there is generally not much point in making arguments within the letter to the editor because no one except the editor will ever read it. It is always best to try to do something to the ms so that that reviewer and others of like mind will be happier when they read the revised ms. Ideally, we respond by making a modest adjustment to the ms, and just paste that into the appropriate point in the response letter. We want to make it easy for the editor to conclude that we have been reasonable and responsive. (Remember that the reviewers will undoubtedly read the published paper later, and perhaps will see your letter of response during the next stage of review.) Start with the easy criticisms and work toward the harder ones. Similar critiques that show up in two or more reviews inevitably require meaningful changes. In your letter of responses, substance, tone, and style all matter. At the first reading of reviews critiquing my work, I am inevitably disappointed at the intellectual acumen of the reviewers ("What's the matter with this person?!"), but every paper I have been involved in was improved by the reviews and revisions. I have a personal rule that I set aside troubling reviews for a couple weeks before trying to respond. Use your coauthors to help decide which battles are and are not worth fighting.

Following are some of my favorite examples showing how NOT to respond to reviews.

"The fact the reviewer does not understand the Friedman test [is not our fault]".

"If the referee were familiar with the literature then he would already know that ...".

"This is another example of the referee presenting a passionate argument about a subject that he/she obviously has little understanding of."

"This comment is also completely erroneous ... [the reviewer] obviously did not really read the paper which we submitted.

"It is difficult to understand how the referee became so confused about this."

Following are responses to reviews from some manuscripts that I have worked on. At the end are the actual reviews. All of the papers were ultimately accepted. You can see the final version of the manuscripts at the links below. Watch the footers to see which section you are in.

Lombardero, M.J., P. Vázquez-Mejuto, and M.P. Ayres. Role of plant enemies in the forestry of indigenous versus nonindigenous pines. *Ecological Applications*, in press.

<http://www.dartmouth.edu/~mpayres/pubs/abs71.htm>

Reynolds, L.V., M.P. Ayres, T.G. Siccama, and R.T. Holmes. 2007. Climatic effects on caterpillar fluctuations in northern hardwood forests. *Canadian Journal of Forest Research*, in press. <http://www.dartmouth.edu/~mpayres/pubs/abs64.htm>

Tran, J.K., T. Ylioja, R. Billings, J. Régnière, and M.P. Ayres. 2007. Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis* (Coleoptera: Scolytinae). *Ecological Applications*, in press.

<http://www.dartmouth.edu/~mpayres/pubs/abs65.htm>

Pureswaran, D.S, B.T. Sullivan, and M.P. Ayres. 2006. Fitness consequences of pheromone production and host selection strategies in a tree-killing bark beetle (Coleoptera: Scolytinae). *Oecologia*, in press.

<http://www.dartmouth.edu/~mpayres/pubs/abs62.htm>

Ylioja, T., D. H. Slone, and M. P. Ayres. 2005. Mismatch between herbivore behavior and demographics explains scale-dependence of host susceptibility in two pine species. *Forest Science* 51: 522-531.

<http://www.dartmouth.edu/~mpayres/pubs/abs54.htm>

Lombardero, M.J., M.P. Ayres, and B.D. Ayres. 2006. Effects of fire and mechanical wounding on *Pinus resinosa* resin defenses, beetle attacks, and pathogens. *Forest Ecology & Management* 225: 349-358.

<http://www.dartmouth.edu/~mpayres/pubs/abs58.htm>

*Matt Ayres*

MS# 07-1048 -- Revised for *Ecological Applications*

“Herbivory and the forestry of indigenous versus nonindigenous pines”  
by María J. Lombardero, Patricia Vázquez-Mejuto, and Matthew P. Ayres

**Responses to reviewers**

**26 December 2007**

Our thanks to the reviewers and the subject editor for thoughtful critiques of our manuscript. We have adopted all of the suggestions, including clarifying the relationship between our study and the broader literature on the enemy release hypothesis. We think that the manuscript has been greatly improved by these revisions and we hope that you will now find it suitable for publication in *Ecological Applications*. Our point-by-point responses to comments are detailed on the following pages.

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Queries/critiques are numbered and in blue Times Roman font. Responses follow in black Arial font. Revised prose from within the ms is in red Arial font.

### Detailed responses to Subject Editor

1. ... study does not actually examine the enemy release hypothesis. We were surprised to read this in the reviews, but of course it is a fair point and we were happy for the chance to eliminate this weakness. In considering our response, we did a careful review of the literature on ERH. There was some confusion that we had not appreciated. There is some added value to our revisions in helping to sort out different ways in which ERH has been treated. There are presently about 80 papers that deal explicitly with ERH, the majority of which are as reviewer 2 interpreted ERH. But about a quarter of them dealt as we did with the notion that nonindigenous species are expected to suffer less from enemies than similar indigenous species in the same community. The appendix to this letter contains the citations and abstracts for ten of these papers that have recently been published in pretty good journals; we highlighted the relevant sentences. A few papers (e.g., Colautti et al. 2004 and van der Putten 2005 in appendix) treat these as two distinct predictions that both flow from ERH, which is the position we have taken. The core of our response is within the following paragraph from the revised introduction.

“The idea that populations might suffer less damage from biotic enemies when they occur outside their historical range has a long history (Darwin 1859, Elton 1958), but has recently been formalized as the Enemy Release Hypothesis (ERH; Williamson 1996, Crawley 1997) and has received considerable interest because of its relevance to invasion ecology (Keane and Crawley 2002, Stamp 2003, Colautti et al. 2004, Hierro et al., 2005). One prediction of ERH is that biotic enemies will have less impact on populations that have become established outside their indigenous range compared to populations of the same species occurring within their historical distribution (e.g., DeWalt et al. 2004, Cripps et al. 2006, Ishtiaq et al. 2006). This prediction is a foundation for biological control programs (Vila et al. 2005) and for the theory of evolution of increased competitive ability (Blossey and Notzold 1995, Stastny et al. 2005). Another prediction, or perhaps extension, of ERH is that nonindigenous populations will experience less damage from enemies than similar indigenous species with which they now co-occur (Agrawal et al. 2005, Cappuccino and Carpenter 2005, Liu et al. 2007). This latter prediction is of particular relevance to plant invasions because of the frequent importance of interspecific competition (Lau and Strauss 2005, Moorcraft et al. 2006, Epstein and Molofsky 2007). Here, we highlight its additional relevance for foresters who might choose to propagate either indigenous or nonindigenous tree species. To avoid confusion with the broader sense of ERH, we refer to this specific theoretical prediction as “enemy reduction in nonindigenous species” or ERNS.”

2. A change in the title also appears appropriate. The new title is: “Role of plant enemies in the forestry of indigenous versus nonindigenous pines”
3. The Introduction ... will require substantial changes to ... set the context ... in terms of ... introduced species. In addition to changes in the introduction, we have made corresponding adjustments to the abstract and discussion. The abstract and key words still reference ERH because this seemed appropriate given the precedent in previous papers and the clarified logic in this paper. As suggested by the reviews, we have also substituted “indigenous” and “nonindigenous” for “native” and “introduced” (or “exotic” or “non-native”).

4. Confusion about plot and stand... We were using plot and stand interchangeably. Thanks to the reviewer for noticing. We now use “stand” throughout except for describing the surveys of fungal damage where we employed plots within a few of the largest stands. “In most cases, we did this by examining each tree within the stand, but in the three largest stands, we scored 100 trees within a randomly located plot within the stand.”
5. more information about the plots would be good, such as size, number of trees, and criteria for location within a stand. On line 183 (p. 9) it would be helpful to know how many trees were in the plots in order to have some idea of the sample sizes for number of infected trees. Methods: Study Area now includes the following information about stands: “... usually <1 ha ... trees were planted 2.5 m apart in rows separated by 3 to 3.5 m (usually 50 – 400 trees per stand).”
6. More needs to be said about the fungal attack (perhaps this should be in the Introduction), and it would be nice to know if the fungus is native. Intro now includes the following. *Sphaeropsis sapinea* (Fr.) Dyko and Sutton (Diplodia tip blight, formerly *Diplodia pinea* (Desm.) Kickx) is a fungal pathogen of pines. It is presumed to be indigenous to western Europe since it was first described from France in 1842. Nowadays, *S. sapinea* appears to be globally present wherever there is *Pinus* and it can be a consequential pathogen for numerous pine species in numerous ecosystems across the world (de Wet et al 2000). Normally the fungus enters the plants through small wounds (e.g., from insects or weather damage) and then invades the tissue, causing dieback of the shoots and the death of the trees. Our studies included measurements of *S. sapinea* damage because we could see that it was present and because of its potential association with bark beetles.”
7. Figures 4 and 5 need more complete explanation in the legends (comment of Reviewer 1), and the text about these figures could use some clarification. The error bars are  $\pm 1$  SE. This is indicated within the figures.
8. The Discussion needs ... to clearly set the work in the context of ideas about introduced species and the enemy release hypothesis. ... could be reduced somewhat in length, ... For example, the two paragraphs on lines 292-322. Discussion has been modified to reflect our responses to #1 and #3 above. The two paragraphs have each been shortened by 4-6 lines.

## Detailed responses to Reviewer #1

9. ... study the current title is too restrictive. I suggest it be recast to address ERH in broad terms. See response to #2.
10. Much hinges ... on knowing that the lumber yard was indeed the source of the bark beetles. This is quite well known in general, and we could verify it in this study in particular. Methods now include the following: "Occasional timber yards provide a source of large numbers of *T. piniperda* that arrive with the logs and emerge and disperse into the landscape before the logs are sawed (Långström and Hellqvist 1990; Borkowski 2001).... Examination of the log yard verified the presence of large numbers of *T. piniperda*; the study area contained no other comparable sources of *T. piniperda*."
11. what is a "plot"? See response to #4.
12. no mention [fungus] in the Introduction) ... as whether it is known if *S. sapinea* is a native fungus in Spain... See response to #6.
13. How were the main branches selected [1 164]? Same question for branches measured in line 193. They were selected at random from within each tree. This has been specified at both points within the ms.
14. I do not understand the rationale for measuring shoot size for shoots that had fallen from trees. The methods now include the following. "In the same stands, to compare the plant tissue lost per attack by *T. piniperda*, we measured the diameter and length of 106 *P. pinaster* shoots and 102 *P. radiata* shoots that had broken off at the point of *T. piniperda* attack and fallen to the ground (17 to 53 shoots per species per stand)."
15. line 332-334. No quantification is provided to back up the statement on the stout needles of *P. pinaster* compared with the long needles of *P. radiata*. This is a very important omission as the greater loss of PS tissue in *P. radiata* compared with *P. pinaster* is central to the argument here that the ERH is only operating with respect to some parameters (% trees attacked) but not others (extent of damage to each tree). This was a misunderstanding from some imprecise writing (and was related to #14 above). The argument is with respect to the size of shoots not needles. This has been clarified in the discussion as follows. "... a larger fraction of photosynthetic tissue is lost per beetle attack in *P. radiata* than in *P. pinaster*. The species are alike in that photosynthesis occurs within repeated similarly sized modules of needle-bearing shoots that extend from growing branches. Following an attack by *T. piniperda*, the shoot distal to the point of attack dies and falls to the ground, along with the needles that it held. However, the average length of these lost shoots is markedly longer in *P. radiata* compared to *P. pinaster* (17.1 vs. 10.6 cm, respectively). This is because the shoots of *P. radiata* are relatively slender compared to *P. pinaster*, and *T. piniperda* preferentially attacks where the diameter is 5 – 6 mm, presumably because this matches the size of the internal feeding gallery required by the insect (see also Haack et al. 2001). Since more of each shoot is lost per beetle attack in *P. radiata* compared to *P. pinaster*, a larger proportion of photosynthetic tissue is destroyed with the same proportion of shoots attacked."
16. Figs, 4 & 5 cannot be critically evaluated as neither has explanation as to the apparent error terms about the means for diameter, height of trees in the plantations. Are these SE? SD? Other?. See response to #7.
17. "debunk" in the abstract is too strong. Agreed. This has been changed.

## Detailed responses to Reviewer #2

18. major shortcoming ... define the enemy release hypothesis (ERH) differently than it is commonly and historically used. See responses to #1 and #2.
19. If the author are aware of documentation that supports tree plantations to minimize losses to enemies, they should provide it. This notion has been specifically advanced by Sedjo 1983, Zobel et al. 1987, Gadgill and Bain 1999, and Wingfield 2003. We found and added Sedjo as a result of this prompting. Sentences within the ms have been adjusted to clarify the nature of this documentation. From 1<sup>st</sup> para of intro: "On the other hand, there might be advantages to nonindigenous trees if they have been separated from their native herbivores and pathogens (Sedjo 1983, Zobel et al. 1987, Gadgill and Bain 1999, Wingfield 2003)". From last para of discussion: "The enemy release hypothesis suggests the attractive prospect of high yield silviculture via escape from plant pests (Gadgill and Bain 1999, Wingfield 2003). There is ecological merit to the concept, as illustrated by our results (Figure 2), and the social and economic benefits can be considerable (Sedjo 1983, Toro and Gessel 1999), at least in the short term."
20. line 26: or because of previous commercial experience? e.g. copycat planting. We agree that we cannot know how important the enemy release hypothesis has been in the choice of tree species. Instead we say that there is literature describing ERH as a rationalization that has been offered in favor of planting nonindigenous trees (#19). . From abstract: "one rationalization has been that silvicultural productivity is enhanced when trees are separated from their native herbivores and pathogens."
21. line 62: insert: 'are assumed to' in between they and have. To accomplish the same with fewer words we substituted the word "if" for "because": "...there might be advantages to introduced trees if they have been separated from their native herbivores and pathogens"
22. line 82: could the NIS be adapted to the enemy if they did not coevolve?. We meant the opposite. The sentence has been clarified and now reads: "...plants may become adapted to their historically important herbivores such that growth losses are minimized".
23. lines 123-124, 128: references?. Appropriate references have been added. "... they facilitate the introduction of fungi that may be pathogenic and/or produce staining in the xylem that lowers the commercial value of wood (Seifert 1993)." And "...are relatively rare in southern Europe and restricted to occasional episodes of beetle outbreaks (Långström and Hellqvist 1990, 1993)."
24. lines 326-327: Can you review literature to demonstrate whether the ERH is or is not supported in silviculture around the world? The species is sufficiently well planted, we should be able to discern if it fact this species experiences true release from enemies. Ours is the first such study that we know.
25. line 409-418: you need references for many of the points made in here, as it seems anecdotal as it is presented. The paragraph (last in discussion) has been revised and the points are supported by references.
26. line 420-421: examples of this are numerous e.g. Eucalyptus in different countries introduced with or without herbivores (described in Elton's book). Good point. We now mention eucalyptus and cite Elton.

06-12-AE

Climatic effects on caterpillar fluctuations in northern hardwoods forests by Lindsay V Reynolds, Matthew P. Ayres, Thomas G. Siccama, and Richard T Holmes

**Responses to reviewers**

**9 June 2006**

Our thanks to the reviewers and the associate editor for their thoughtful critiques of our manuscript. We have adopted virtually all of the suggestions, including adding a new response variable based on the recommended autoregressive model and improving the climatic analyses by including data from all long term weather stations in the Hubbard Brook Forest. We think that the manuscript has been greatly improved by these revisions and we hope that you will now find it suitable for publication in CJFR. Our point-by-point responses to comments are detailed on the following pages.



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Queries/critiques are numbered and in blue Arial font. Responses follow in black Times Roman. Revised prose from within the ms is in red Times Roman.

### Detailed responses to AE

1. Identity of Lepidoptera species. Reviewers 1 and 3 asked if the lepidopteran population fluctuations could have been caused by just one or a few outbreaking species. Reviewer 2 questioned lumping all lepidopteran species as simply "caterpillars" and asked if separate analyses could have been done for the most commonly collected families (e.g., Geometridae and Noctuidae). Was any attempt ever made to identify the larvae to family, genus, or species? Were any notes taken on the occurrence of outbreaking species or the lack thereof during the 20 year period? Can any of the analyses be done for just the most commonly collected families, genera, or species? Or alternatively can any of the analyses be done after removing the outbreaking species?

This is a good question. We have addressed it in two ways. The data permitted a comparison of fluctuations in the abundance of geometrids vs. others. This has been added as a **panel to Fig. 1**. The covariation between these groups effectively shows that the patterns are not driven by a single species. We also provide additional information about the diversity of the Lepidoptera community.

*The results now includes:*

**"The abundances of geometrids vs. other families covaried over time (Fig. 1 upper): per capita interannual growth rates of geometrids and others were well correlated ( $r = 0.69$ ,  $p = 0.001$ )."**

We also added a bit more of the relevant natural history. *The methods now include:*

**"All caterpillars were counted, measured, and classified to family. Because we had greatest confidence in the identification of geometrids, we partitioned the data into geometrids vs. all others. Identification of caterpillars to genera or species was not generally possible, because we did not want to remove individuals from the forest, but typically there were 20-40 different caterpillar morphotypes that contributed to the abundance estimates each year (R.T. Holmes, unpublished data). During 1969-70, there was an outbreak of *Heterocampa guttivita* (Notodontidae) in HBEF, but within our time series there have been no insect outbreaks or defoliations that would have been noticeable in a forest health survey, nor any years in which caterpillar abundance was conspicuously dominated by one or two morphotypes (R.T. Holmes, unpub. observations). The forest at HBEF probably contains at least 50 species of Lepidoptera that are reasonably abundant most years and presumably appeared in our sampling (Covell 1984, Wagner 2005, E.E. Stange, pers.comm.)."**

2. Analyses of winter temperatures. Reviewer 1 suggested a figure showing the relationship between winter temperatures and caterpillar survival. Reviewer 2 questioned analyzing the "lowest minimum daily temperature" as the most extreme weather event affecting insect survival, rather than perhaps the lowest 5-7 day running average of minimum daily temperatures and suggested considering the entire period October-April as the "overwintering period" rather than analyzing separately the coldest periods during the three seasons of fall, winter, and spring, Reviewer 3 if extreme cold events in spring might be more important to insect survival than during winter,

As suggested, we have added to Fig. 2 a panel showing R vs minimum winter temperature. The reviewers are correct that there are many metrics of winter cold that could be evaluated. Actually, there are innumerable possibilities. The discussion is now more explicit in stating this, and explaining why we have chosen to analyze minimum winter air temperature for the present research question.

*The relevant paragraph in discussion has been expanded as follows:*

“Interannual changes in caterpillar abundance were uncorrelated or negatively correlated with minimum winter air temperature (Fig. 2, upper; Table 1), which argues against the importance of cold-induced mortality of overwintering lifestages in generating the interannual fluctuations in caterpillar abundance (Fig. 1). We cannot readily explain the significant negative correlation between minimum winter temperature and  $\varepsilon_t$  (Fig. 3, Table 1) because it was opposite the hypothesized direction. Nor can we explain why the pattern was evident with  $\varepsilon_t$  but not  $R_t$  because it is unclear what mechanisms produce the density-dependence that was removed from  $R_t$  to calculate  $\varepsilon_t$ . Minimum winter temperature may be correlated with another factor that influences overwinter survival (e.g., snow cover, which might be more important than air temperatures as a determinant of temperatures experienced by insects that overwinter in the litter layer; Kukal et al. 1991, Lombardero et al. 2000a). Also, although the minimum temperature is commonly important for winter survival of insects, there can also be mortality from relatively modest cold in the spring or fall when insect are not winter acclimatized (Bale 2002). We could not provide tests for effects of winter cold that depend on acclimatization and overwintering habitat because we presently lack adequate knowledge of species-specific overwintering biology. On the other hand, environmental effects that vary among species are less likely to influence the abundance of caterpillars in general.”

3. Time series analyses. Reviewer 1 suggested some alternative analyses and wondered about the statistical power of some of the tests that were employed, Reviewer 2 questioned the statistical approach used for the time series analyses and the tree-ring analyses.

The reviewers are correct that an autoregressive approach to the analysis could indicate different interpretations. As suggested, we have conducted analyses with an autoregressive model and included them in the paper. No conclusions were affected except that a negative correlation emerged between minimum winter temperature and  $\varepsilon$ . See #25 for responses regarding power.

*The methods now include:*

“To test for climatic effects on caterpillar fluctuations, we calculated correlations between both climatic metrics and the per capita growth of caterpillar populations from year  $t$  to year  $t + 1$ :

$$R_t = \ln(A_{t+1}) - \ln(A_t) \quad \text{eqn 1}$$

Where  $A_t$  = abundance at time  $t$ ,  $A_{t-1}$  = abundance at  $t-1$ . An alternative approach is to test for relationships between climate and residuals from the autoregressive model:

$$\ln(A_{t+1}) = \beta_0 + \beta_1 \cdot \ln(A_t) + \varepsilon_t \quad \text{eqn 2}$$

where  $\beta_0$  and  $\beta_1$  are parameters fit to the data (which reflect density-dependent processes), and  $\varepsilon_t$  are the residuals (Miller et al. 1989, Royama 1992). We report results from both analyses.”

*The results include the following changes:*

“Temporal dynamics of caterpillar abundance suggested the presence of negative feedback (density-dependence): from eqn 1,  $R_t$  was negatively correlated with  $A_t$  ( $r = -0.67$ ,  $p = 0.0018$ ) and from eqn 2,  $\ln(A_{t+1})$  was only weakly related to  $\ln(A_t)$  ( $\beta_1 \pm \text{SE} = 0.12 \pm 0.24$ ,  $p = 0.62$ ). Subsequent analyses involving  $\varepsilon_t$  and  $R_t$  represent tests for environmental effects on caterpillar fluctuations either with or without this apparent density-dependence removed, respectively.

At station #1, which was nearest in elevation to the HBEF caterpillar study site, minimum air temperature ranged from -18 to -30 °C from the winters of 1986-87 to 2003-04 (mean  $\pm$  SD = -25  $\pm$  3). Adiabatic effects on minimum winter in the HBEF averaged 0.5 °C / 100 m ( $r^2 = 0.98$  for average minimum temperature vs. elevation,  $n = 4$  stations). Contrary to the theoretical

prediction, mild winter extremes tended to be uncorrelated or negatively correlated with fluctuations in caterpillar abundance: for  $R_t$ ,  $r = -0.21$  and  $p = 0.40$ ; (Fig. 2 upper); for  $\epsilon_t$ ,  $r = -0.61$  and  $p = 0.007$  (Table 1).”

4. Reviewer 3 questioned the value of using tree ring growth as a surrogate for tree chemistry. Actually there are very strong theoretical and empirical bases for anticipating a negative phenotypic correlation between plant growth and phytochemical suitability for herbivores. We have clarified this by reference to a meta-analysis and four other reviews (Herms and Mattson 1992, Awmack and Leather 2002, Herms 2002, Stamp 2003, Throop and Lerdau 2004).

*Introduction includes the following:*

“Many experimental studies have demonstrated phenotypic plasticity in the nutritional suitability of foliage for herbivores (Herms 2002, Throop and Lerdau 2004, and references within), and commonly, environmental conditions that promote plant growth (e.g., easing of nitrogen limitations) also promote the production of foliage with higher nitrogen content and lower carbon-based secondary metabolites (see meta-analyses of 55 – 174 fertilization studies by Koricheva et al. 1998). Frequently, these phytochemical changes translate into higher nutritional suitability for herbivores (Herms and Mattson 1992, Erelli et al. 1999, Awmack and Leather 2002, Stamp 2003, Moore et al. 2004, Hale et al. 2005).”

5. Reviewer 1 questioned whether univoltine lepidopterans are ever “time stressed” especially if they are spring feeders.

The reviewer is correct that this is an implausible scenario for spring feeders. Now we say so.

Our point remains valid for species that feed in late summer. *Discussion now says:*

“Longer growing seasons might enhance the probability that insects can complete development to a lifestage that is adapted for surviving the winter: e.g., pupae in *Papilio canadensis* (Papilionidae; Ayres and Scriber 1994, Kukal et al. 1991) or 2<sup>nd</sup> or 3<sup>rd</sup> instars (early larvae) in many species of *Choristoneura* (Tortricidae; Han and Bruce 1998, Graether et al. 2000).

However, the numerous species that feed in the early-season (e.g., *Alsophila pometaria*, Geometridae, Hunter 1995) are unlikely to be constrained by development time.”

6. Reviewer 3 questioned if lepidopteran numbers on understory trees is always a good indicator of caterpillar numbers in the canopy.

*Our methods now include the following:*

“Sampling was conducted in the forest understory (0.5 – 3 m) because previous research in these study sites indicated that caterpillar abundance in the lower canopy is representative of caterpillar abundance in the upper canopy (Holmes and Schultz 1988).”

7. Reviewer 3 questioned if the caterpillar biomass data could be analyzed separately in terms of spring feeders (the first two sampling dates) and summer feeders (the last two sampling dates),

See response #39.

8. Reviewer 3 also pointed out that this study did not measure natural enemy levels or the length of the summer season, and therefore care must be taken when addressing these topics in the paper.

See response to #43.

9. AE would like the authors to add more details as to how caterpillars were searched for and collected.

*The methods now include the following:*

“The transects were parallel and separated by 50 m. Searches at each point included 100 leaves of both *A. saccharum* and *Fagus grandifolia* (the most common understory tree species) at 0.5 - 3 m above ground. Leaves were chosen from the nearest tree or shrub to the sampling point. All leaves in a sample were on the same plant unless the plant had fewer than 100 leaves, in which case we would continue sampling leaves on the next closest plant to the

sampling point. Leaves were inspected by searching the top and carefully turning each leaf over to inspect the underside, leaves were not removed from the plants.”

10. AE asked if we have any temperature data to show how closely the interior forest sites that you sampled matched the data at the HBEF headquarters?

Thanks. We have improved the climatic analyses by using all 3-4 climate stations in HBEF that have data for the period of interest. We have also included comparisons of HBEF records with air temperatures that we collected from the forest understory. *The methods now include the following:*

“Using historical air temperature records from the Hubbard Brook Experimental Forest ([www.hubbardbrook.org](http://www.hubbardbrook.org)), we evaluated two metrics that were hypothetically related to caterpillar population fluctuations: (1) minimum winter air temperature, which was considered to be the lowest minimum daily temperature recorded between 15 October of year  $t$  and 15 April of year  $t+1$ , and (2) the annual thermal sum (cumulative degree days above a 5° C base from 15 March to 15 October), which was taken as a measure of development potential in Lepidoptera. The temperature records from HBEF include four weather stations that have been recording daily minima and maxima since at least the start of the caterpillar time series in 1986: station #22, near headquarters at 253 m asl; #1, near watershed 1 at 488 m asl; #6, near watershed 4 at 747 m asl; and #14 in watershed 7 at 728 m asl. The first years of complete records were 1957 for #22 and #1, 1961 for #6, and 1965 for #14. Because most moths are quite mobile, and our hypotheses involve regional effects on caterpillar abundance, we used all of these stations to estimate a single measure for each year (of both minimum winter temperature and thermal sum) for HBEF as a whole. To do this, we calculated the residuals for each station in each year relative to the long term average for that station, and then averaged the residuals of the four stations for each year. Departures of the residuals from 0 represent years that were relatively warm or cold across the HBEF. Thermal sums were incremented at 3-hour intervals by interpolation from daily maxima and minima using a half-sine function; thermal sums calculated in this way were  $\pm 2\%$  ( $r^2 = 0.995$ ) of thermal sums calculated without interpolation from nine temperature series for which we had complete hourly records (summers of 2004 and 2005 for 1-2 climate stations at three of our study sites; E. Stange, unpublished data). Air temperatures from HBEF station #1 were highly correlated with air temperatures in the forest understory where caterpillars were studied;  $r^2 = 0.98$  for daily minima, maxima, and averages from HBEF records vs. measurements by us at 1 m height in the forest understory (1.3 km south of #1 at 432 vs. 488 m asl; our measurements from 21 May to 31 December 2004 with Type T thermocouples and a 12-bit datalogger, HOBO® U12, Onset Computer Corporation, Bourne, MA, USA; mean  $\pm$  SD of the differences (#1 - our site) =  $-0.6 \pm 1.0$ ,  $1.1 \pm 1.6$ , and  $0.4 \pm 1.1$  °C for daily minima, maxima, and averages,  $n = 225$  d.”

*The results include the following:*

“At station #1, which was nearest in elevation to the HBEF caterpillar study site, minimum air temperature ranged from -18 to -30 °C from the winters of 1986-87 to 2003-04 (mean  $\pm$  SD =  $-25 \pm 3$ ). Adiabatic effects on minimum winter in the HBEF averaged 0.5 °C / 100 m ( $r^2 = 0.98$  for average minimum temperature vs. elevation,  $n = 4$  stations). Contrary to the theoretical prediction, mild winter extremes tended to be uncorrelated or negatively correlated with fluctuations in caterpillar abundance: for  $R_t$ ,  $r = -0.21$  and  $p = 0.40$ ; (Fig. 2 upper); for  $\epsilon_t$ ,  $r = -0.61$  and  $p = 0.007$  (Table 1).

Per capita changes in caterpillar biomass from year  $t$  to year  $t+1$  were positively correlated with the thermal sum in year  $t$  (Fig. 2, middle;  $r = 0.56$ ,  $p = 0.012$  for  $R_t$ ,  $r = 0.49$ ,  $p = 0.032$  for  $\epsilon_t$ , Table 1). Adiabatic effects on thermal sums in the HBEF averaged -75 °C d / 100 m ( $r^2 = 0.99$  for average thermal sum vs. elevation,  $n = 4$  stations). From 1961 to 2004, average thermal sums in HBEF increased by 153 °C d (Fig. 3), which was 8 - 10 % of the 44-year

averages of 1549 – 1898 °C d at 253 – 747 m asl. This warming trend was also evident in the longer time series (1957 – 2004) available for stations #1 and #22 (slope  $\pm$  SE =  $3.1 \pm 1.0$  °C d / year,  $p = 0.004$ ,  $n = 48$  years), and the time series for four stations from 1965 – 2004 ( $3.8 \pm 1.2$  °C d / year,  $p = 0.004$ ,  $n = 40$  years). In contrast, there have been no time trends in minimum winter temperature (slope  $\pm$  SE =  $0.035 \pm 0.028$  °C / year,  $p = 0.22$ ,  $n = 44$  years), although the minimum temperatures during 2000-01 and 2001-02 were the mildest since 1958 at 5.2 and 6.9 °C warmer than the long-term average.”

11. AE asked how much annual variation occurred in degree-day accumulation at the start of your sampling. ... Can you prepare a figure that shows how many degree days were accumulated by June 1 and July 1 by year during your study period of 1986-2005? Is there any relationship between caterpillar biomass and heat sums as of June 1?

Good idea. Thermal sums at all dates look about like Fig. 3, but the slopes of the warming trend increase steadily (reflecting contributions to the warming trend from spring through autumn). *We added the following to the legend of Fig. 3:*

“This has involved a warming trend throughout the spring, summer, and fall. For an intermediate elevation of 496 m asl, estimated mean thermal sums ( $\pm$  SD) on 1 June, 1 July, 1 August, 1 September, and 15 October were  $287 \pm 61$ ,  $621 \pm 60$ ,  $1040 \pm 70$ ,  $1555 \pm 79$ ,  $1739 \pm 99$  °C days, respectively. The corresponding estimates of warming trends (°C days / year  $\pm$  SE) were  $1.5 \pm 0.7$ ,  $1.7 \pm 0.7$ ,  $2.0 \pm 0.8$ , and  $3.0 \pm 0.8$  ( $p < 0.05$  for all); the increasing slope of the warming trend with Julian date was significant at  $p = 0.023$ ,  $r^2 = 0.95$ ,  $n = 5$ .”

## Detailed responses to Reviewer #1

12. p 2 | 5 and p 3 | 23 - accelerated insect development due to high temperatures does not usually lead to increased fecundity, you properly discuss this below but I think you should avoid creating a wrong impression also here.

We now have avoided giving this impression in the abstract and introduction by deleting a few phrases about fecundity in the explanation of our predictions. *The relevant section in the abstract now reads:*

“(H2) long, warm summers accelerate insect development rates and enhance survival; and (H3) interannual climatic variation influences the growth and physiology of dominant host trees, which affects leaf chemistry (caterpillar diet), which in turn influences larval survival and caterpillar fluctuations.”

*The relevant section in our introduction now reads:*

“ Second, rates of growth and development are temperature dependent in most insects, including Lepidoptera larvae (Sharpe and DeMichele 1977, Huey and Kingsolver 1989, Ayres and Scriber 1994, Gilbert and Raworth 1996, Bale et al. 2002, Gillooly et al. 2002, Powell and Logan 2005), thus the developmental success of caterpillars might be influenced by summer temperatures when caterpillars are feeding.”

13. p 2 | 7 - make it clear that you did not test for increased survival, fecundity etc.

See response to #12.

14. p 2 | 17 and p 12 | 3. I do not exactly understand “broad driver” (what would be the opposite, a narrow driver?) - I admit that this may be due to my poor knowledge of English but may you still consider a more explicit formulation?

Our term “broad driver” refers to the idea that these caterpillar populations are fluctuating synchronously over a large spatial scale, and thus must have some driver that acts over a similar large (broad) spatial scale. To clarify, we now say “broad-scale driver” instead of “broad driver”. *The relevant section in our abstract now reads:*

“ In hardwoods forests of the northeastern U.S., there is some broad-scale driver (at least partly related to summer temperatures) that generates interannual dynamics in caterpillar abundance.”

The relevant section in our discussion now reads:

“ Our results indicate that there is some broad-scale driver (at least partly related to summer thermal accumulation) that generates dynamics in caterpillar abundance in these northern hardwood forests.”

15. p 3. I would also mention that the ranges of many Lepidopterans readily respond to climatic changes (like global warming), we see it but do not understand why.

Done. *The relevant section in our introduction reads:*

“ In addition, it has been noted recently that the ranges of several species of Lepidoptera have shifted in response to climate change, but the mechanisms operating behind these shifts are poorly understood (Parmesan et al. 1999, Parmesan 1996). In general, the mechanisms by which climate influences interannual fluctuations in Lepidoptera abundance are not clear.”

16. General. I understand that you did not identify your larvae. However, might it have been the case that some peak values were created by one single outbreaking species, *Alsophila pometaria*, for example? Possible confounding effects of such scenario should be discussed.

General. I understand that your time series are not long enough to facilitate the application of proper time series analyses. However, may it still be possible to somehow consider internal (i.e. top-down driven, in the present context) dynamics of insect populations? What about including the density of the previous year in your analyses? I perfectly understand that to calculate correlations between initial values and increments is statistically flawed and density-dependence cannot be studied in this way. However, I have always been wondering if we can include initial values as covariates when studying the dependence of the increments on something else, i.e. would the initial values function as proper covariates even if the

tests associated with the initial values themselves would be wrong (if you know the answer, might you consider e-mailing me :-)). In any case, I would welcome a short discussion of possible consequences of ignoring autocorrelations in moths densities in this paper. What about two-way analyses etc, why not to include winter and summer temperatures in a single model?

See responses to #1-3.

16. a General. I do not know much about trees and I do not know anything about forestry but I would guess that patterns of spatial autocorrelations in tree growth rates should be well known in general? If this is the case, then why to put so much effort in studying this question here?

The evidence for spatial autocorrelation in tree growth rates in northeastern hardwood forests is surprisingly equivocal. *We address this in our discussion:*

“Some dendrochronology studies in New England have reported interannual variation in tree growth that seemed attributable to climate (Lyon 1936, Goldthwaite and Lyon 1937, Lyon 1940, Cook and Jacoby 1977). However, we are not the first to report that tree growth in this region is not always responsive to climatic variation (Avery et al. 1940, Kirkpatrick 1981). Tardif et al. (2001) also noted a lack of stable correlations between climate and radial growth in *A. saccharum*, *Fagus grandifolia*, and *Tsuga canadensis* in nearby Quebec.”

17. P 4 | 25. Any idea about the number of sp involved?

See response to #1

18. p 6 | 16. lowercase americana.

Done.

19. p 6 , tree cores. Remind shortly why was all this done, the reader has likely forgotten the respective sentence in the introduction by now. Also remind p 7 | 23 what was the rationale of the statistical analysis, what were you looking for? Moreover, may the presentation of the tree core stuff be too detailed? I try to follow the guideline that the amount of text allocated to a question should be roughly proportional to the importance of the question, now I see a slight imbalance here (also in Discussion, but I also understand that this is a forestry journal!), e.g. is it really necessary that the reader knows the magnification of your lense (p 7 | 4)?

*We added this sentence to the beginning of the methods section about tree cores:*

“ To address whether caterpillars are influenced indirectly by climate through their food resources, we analyzed tree growth in two species of host trees.”

20. Results, beginning. Can you report your total sample size in terms of absolute numbers of individuals? Just to achieve better visualisation.

Done.

21. p 8 | 2. As the effect of winter temperature on moth survival is likely non-linear, I would like to see a graphical presentation of the relationship. Moreover, if the  $r=-0.21$  were the true value, it would likely be ecologically meaningful, so I think you should avoid a too clear-cut no-effect-judgement, and it would be appropriate to complain about low statistical power here.

Figure is now shown.

22. p 8 | 3. be consistent in presentation: if you report  $r$  for winter temperature, do not report  $r$ -square for summer, just to make the values easier to compare.

Done.

23. p 8 | 8. here and elsewhere (Table 1, Fig.2) - I would definitely understand “growth rate of caterpillars” as referring to individual growth, say this in a different way.

Thanks. Throughout “growth rate” has become “changes in caterpillar abundance”.

24. p 8 | 11-12. May comparing tree species be irrelevant here?

The comparison is brief and seems relevant to describing the biology of our study trees. *From results:*

“Average growth rates were slightly, but significantly, higher for *A. saccharum* compared to *B. alleghaniensis* (1.76 vs. 1.51 mm / year;  $F_{1,72} = 5.03$ ,  $P = 0.028$ , Table 2).”

25. p 8 | 19-22. Any analysis of statistical power is always very welcome but I am afraid that the way you do it here is not particularly informative. Would you be able to give e.g. confidence limits to cv?

What a good idea. We deleted the old sentence and modified an existing sentence as follows.

*The discussion includes:*

“There was a significant effect of year but it only accounted for a small amount of variation in tree growth: coefficient of variation = 5 % with 95% confidence limits around CV of 4.4 to 6.9 % ( $F_{41,72} = 2.54$ ,  $P = 0.0001$ , Table 3, Fig. 5)”

26. p 9 | 7. “results are unusual” sounds strange. First, rather is this your approach that is original than your results, and, second, - admitting that this may fully be the consequence of my poor English - “unusual” sounds too negative for me. May “original” or “unique” sound better?

Done. *Now the discussion says:*

“There is extensive application of degree-day models to predict the phenology of plants and insects (e.g., Ellsworth and Herms 2004), but our results are different in linking insect population dynamics to thermal sums. “

27. p 9 | 10\_15. Here I disagree. A normal univoltine herbivorous lepidopteran is never time\_stressed in our latitudes, reaching the overwintering stage is never a problem. This especially clear for spring feeders like *A. pometaria* that you mention here which pupates in early May in Maryland, and should be ready at least by early June in your area. You may see e.g.

Tamaru, T., Ruohomäki, K. & Saloniemi, I. 1999. Within\_season variability of pupal period in the autumnal moth: a bet\_hedging strategy? \_ Ecology, 80:1666\_1677.

Tamaru, T., Tanhuanpää, M., Ruohomäki, K. & Vanatoa, A. 2001. Autumnal moth \_ why autumnal? \_ Ecological Entomology, 26: 646\_654

even if I understand that this is not so relevant here but just happy to advertise :\_).

See Response #5.

Moreover, there are definitely many sp that are facultatively bivoltine in your area, so “might” is far too soft. For those spp, indeed, reaching the right stage before winter is crucial.

Done. *Now discussion says:*

“However, the numerous species that feed in the early-season (e.g., *Alsophila pometaria*, Geometridae, Hunter 1995) are unlikely to be constrained by development time. Some Lepidoptera in our study system, e.g., *Orgyia leucostigma* (Lymantriidae) are facultatively bivoltine (two generations per year) in warm years and univoltine in other years, which would double the potential annual growth rate of the population. Also, see response to #5.

28. Table 2. I am in a holy war against excessive numerical accuracy, e.g. in  $P=0.1406$  at least the two last digits represent nothing more than numerical noise.

Thanks!. Fixed.

29. Fig 1. Some internal communication between the authors was forgotten to be deleted.

Done.

All figures. What was the data point used for calculation of SE in each case? Could this be said in the legend shortly enough?

Done



## Detailed responses to Reviewer #2

30. p. 4, "Caterpillar abundance": I am a bit bothered by the lumping of Lepidoptera species as just "caterpillars". Clearly, different insect species have characteristic population dynamics based on individual species ecology. Given the small sample sizes you were working with, I can understand that you could not investigate individual species patterns.

However, if most of the species were Noctuids or Geometrids, I would rather see you analyze the time series for those families separately. Your perspective seems to be more ornithological (i.e., caterpillars as bird food) than entomological.

See response to #1

31. p. 5, "Climate data": I do not agree with your choice of the lowest minimum daily temperature to represent overall overwintering mortality.

The temperature on one day seems a bit too random to characterize such a seasonal phenomenon. I suggest more of an aggregative measure of the effects of low temperatures, for example, a lowest 5-7 day running average of minimum daily temperatures. Longer cold periods are more likely to be relevant to insect mortality than is one 24-hour "snap". Alternatively, you might consider a seasonal accumulation of degree days below some threshold temperature, similar to your degree day sums during the growing season.

Moreover, the "overwintering" period considered (October-April) takes in a lot of insect physiology that includes at least three states:

pre-diapause, diapause, and post-diapause. Cold periods in the fall or spring when insects are entering or leaving diapause may have greater effects on mortality than do much colder ones in mid-winter when the insect is protected by its full diapause physiology. Thus, you might consider three winter variables, essentially some measures of lowest temperatures in fall, winter, and spring.

See response to #2.

32. p. 5, Methods (for caterpillar time series): From the standpoint of time series analysis, correlations using just the population numbers or population increase rates are not really appropriate. Insect population dynamics are usually characterized as "autoregressive processes", in which density at time  $t$  is influenced by densities at times  $t-1$  and (often)  $t-2$ .

(That is, they are first or second order autoregressive processes. See Royama (1992) *Analytical Population Dynamics* for more on this.) In looking at the effects of climatic variables on population dynamics, you need to run correlations on the residuals of the insect time series, after the autoregressive population processes have been filtered out. These residuals approximate the "random" components of the dynamics—that is, perhaps the effects of weather. The methods for such an analysis are described in Miller et al. (1989) *Environmental Entomology* 18: 646-650.

You can use time series procedures in SAS (PROC ARIMA) to compute the autoregressive models.

You used a similar idea in your analysis of the tree ring data.

However, I would suggest running an ARIMA analysis of those data as well.

If they are fit by autoregressive models, I would use those models to compute residuals for the sake of consistency.

See response to #3. We extended the caterpillar analyses as recommended. Our analyses of the tree-ring data are quite conventional for this field. The detrending is analogous to using an autoregressive model, and is quite well justified for these data (Table 2, Fig. 4). We have not changed analyses of the tree ring data.

33. p. 5, l. 8-9 and Table 1. Are the results presented in Table 1 only from HBEF? If so, I would mention this in the table caption.

*Table 1 now says:* "Tree-ring data were for all sites pooled; results are very similar for trees from HBEF only."

34. p.7, l. 23: At the highest abundances, you found less than one half of a gram of caterpillars in a sample of 8,000 leaves collected over the growing season. Is this correct? This seems like an incredibly low number.

From results: "8 - 434 mg / 8000 leaves". These numbers are correct. It must be hard to be a warbler.

35. p. 8, l. 6-8. I am not especially surprised by lack of correlation between insect population growth and tree ring growth. Any connection between tree ring width and the quality of leaves as caterpillar food is tenuous at best. Moreover, defoliating insects as a rule seem to be less affected by host tree physiology than are insects like wood borers. In addition, defoliators—especially caterpillars—are mobile and can easily choose the leaves they wish to eat.

See response #4

36. p. 12, l. 24. This acknowledgement should read "U.S. Department of Agriculture, Forest Service, ..." Done.

37. Fig. 1. Can you show the time series for the other three locations? It would be useful for the reader to see them as well.

The other time series are shorter and have already been published so we do not repeat them here. *This is indicated in the methods:*

"Interannual fluctuations in caterpillar abundance were spatially correlated across these four sites (Jones et al. 2003). Analyses here used only the HBEF caterpillar data because this was the longest time series and because good local climatic data were available."

### Detailed responses to Reviewer #3

38. (1) Pooling of all caterpillars in the biomass estimate. The authors use a single measure, caterpillar biomass, as the dependent variable in all of their analyses. This variable was determined for a site (4 in total) from samples collected from leaves at ten points along each of 4 transects. I have several issues with this variable and think that its use in this paper may obscure interesting patterns, or most critically, could in fact lead to erroneous conclusions about population fluctuations.

First, this variable is a composite of many different species collected over a 2 month period each summer. While a large number of species may be part of this measurement, the majority of the biomass is probably attributable to a relatively small number of species. Thus the relationships found are really reflecting the population dynamics of a few dominant species rather than the lepidopteran community as a whole. I'd like to see a breakdown of the proportion that each species contributes (especially those that are abundant).

Secondly, and most critically in my opinion, is the potential influence of outbreak species on the overall patterns of abundance. The cycles of an outbreak species such as forest tent caterpillar, cankerworms, or saddled prominent could contribute a large portion of the biomass in years when they are abundant. Thus apparent fluctuations in lepidopteran larvae as a composite may simply be reflecting the contribution to the biomass measure

made by the rise and fall of outbreak species. I note that forest tent caterpillar has been very abundant in the northeast US (including, I believe, the area in which this study was conducted) during the time period with the highest biomass and again 10 years earlier (see Fig. 1). If outbreak species were important in these collections and were pooled with the other caterpillars in the composite of biomass, I suggest that they should be removed and the analysis done separately.

In Butler and Strazanac's (2000) Lepidoptera sampling paper, they found that most of the species diversity was in the families Geometridae and Noctuidae (as the authors of this paper also suggested, Page 4, line 24). However, 57% of the total numbers of larvae in the Butler and Strazanac study were gypsy moths. In this manuscript, we are not given a sense of what proportion of the biomass is composed of what species.

Another potentially confounding factor is that some species may increase when outbreak species become abundant. The mechanism behind this pattern is not clear although release from natural enemy pressure because of the abundance of alternative prey (the outbreak species) is one possibility. Lastly, although the authors suggest that caterpillar abundance on undergrowth trees reflects abundance in the canopy, this may not always be true. For example, light to moderate defoliation of the canopy by an outbreak species may force caterpillars of other species down onto the undergrowth trees giving the illusion of densities that are much higher than in other years when the canopy is intact. My main point here is that the presence of one or more outbreak species can have an enormous influence on the pooled estimate of caterpillar biomass. It is critical that the authors document whether fluctuations in the density of outbreak species occurred during the duration of the study. If so, my preference would be separate analyses to remove the contribution of these species. If the authors can not do this (because species identities were not recorded in some or all years), I feel that the utility of this paper will be diminished considerably. Of course, if outbreak species were not important over the duration of the study (and the authors should state this if true), then much of the criticism above will not be valid. The authors need to be much clearer about how the caterpillar data was collected and what the nature of the data is.

See response to #1 and #6. Thanks for a very good suggestion.

39. (2) Pooling of temporal guilds. Lepidoptera in northern temperate forests can be broadly grouped into two temporal guilds, spring and summer feeders. In the analysis of summer temperature, this paper pools four sampling dates (in June and July) into an aggregate measure of Lepidoptera abundance and uses this as the dependent variable. However, this may greatly reduce sensitivity. Although the paper indicates a significant correlation between thermal accumulation and caterpillar biomass, it would be more informative to look separately at these two temporal guilds. Spring feeders are generally regarded to be more influenced by annual variations in temperature than summer feeders (see A.F. Hunter 1991, 1995). Thus, looking at temperature differences across an entire summer on all Lepidoptera may miss critical time periods, such as the first 3 or 4 weeks after bud break which may determine the success or failure of many species in the spring feeding guild. The results of Raimondo et al. 2004 suggest a strong

correlation between population densities of Lepidoptera sharing the same seasonal time period irrespective of feeding habit and host species. Spring-feeding species are often severely constrained to narrow phenological windows by the rapid maturation of foliage. Summer feeders, are somewhat buffered from the effects of cooler temperatures because they are able to feed on nutritionally poorer food and thus have a longer phenological window in which to complete development. Again, my point is that the pooling of Lepidoptera into a single biomass variable will likely obscure some of the critical aspects of temperature that may be present in the data. Such analysis might elevate the importance of the conclusions drawn in this paper.

This is a good idea, but we could not see how to add these analyses without unduly complicating the present paper. We hope to be able to address patterns among various guilds of caterpillars in a stronger way in a future paper.

40. (3) Overwintering temperature. I think that few would be surprised by the finding that there was no significant relationship between low temperature and seasonal abundance of caterpillars. I would submit that the relationship between Lepidoptera and overwintering temperatures is much more complicated than this crude measurement can encompass. While temperature minimums certainly can be lethal, most native insects in the region are going to tolerate all but the most extreme minimums with little problem. A more interesting question might be the time of year when the temperature extremes occur. If the minimum extreme occurs in mid March rather than mid-January, the effect might be considerably more important given that diapause may have been broken and cold tolerance diminished. What about years with big swings between warm and cold (like 2005-2006), or years with extended periods of very warm or very cold winter temperatures? The author's do offer one qualifier, snow depth, which has been documented as being important for some species, such as gypsy moth (see Andresen et al. 2001), but I think discussion of the weaknesses in this very general treatment of winter temperature are warranted.

See response to #2

41. (4) Time lags. There was no examination of the potential for time lags in the analysis of tree growth or winter temperatures on insect populations. While this might be appropriate for winter temperatures (but not necessarily), the response of slow growing trees and their chemical composition may occur on a longer time scale.

Good idea to look for a lag effect from tree growth. There was nothing evident, but *results now include:*

“Neither were changes in caterpillar abundance related to tree growth rates in year  $t-1$  ( $r = -0.25$  to  $0.29$ ,  $p > 0.29$  for relations with  $R_t$  or  $\epsilon_t$ )”

42. (5) Ring growth and tree chemistry. I do not believe that the analysis of ring growth is a particularly good surrogate for tree chemistry. Many studies have shown a high degree of within and between season variance in tree phytochemistry. I submit that using tree ring data to make inferences about primary and secondary leaf chemistry is a stretch. I'd like to see some data or some citations that indicate that this is a valid approach in natural systems. Most of the reference used to support this approach are for studies in highly manipulated, artificial settings, or are review / synthesis papers. None, to my knowledge have empirical data supporting the tree chemistry – growth rate supposition advanced by the authors.

See response #4.

43. (6) The last sentence of the abstract, to me, implies that this study shows that change in caterpillar density influences herbivory levels and the abundance of natural enemies. While this is likely, this study did not examine this question. Rather, it showed only that there was a correlation between caterpillar density and summer thermal accumulation. This should probably be reworded to reflect more accurately what was actually done.

The central role of caterpillars as herbivores, and their influence on bird reproduction and abundance, are well justified for this system. *The intro includes the following:*

“As caterpillars, Lepidoptera are important consumers of plant tissues in these ecosystems (Gosz et al. 1978), and all life stages can be preyed upon to form the base of the grazing food chain (Holmes and Sturges 1975, Holmes and Schultz 1988). Thus changes in Lepidoptera

abundance affect herbivory levels as well as resources for high order consumers, such as insectivorous birds (Holmes and Sherry 2001), which influences their abundance (Nagy and Holmes 2005). “

With such strong evidence from related papers, it seems appropriate to conclude the abstract with reference to ecological connections that go one step beyond the new data presented here. We have not changed the abstract sentence.

44. (7) Hypothesis 2 is phrased as “ long, warm summers.....”. In fact, the authors did not test for changes in summer length but only for thermal accumulation. Thermal accumulation could be the same in a short, hot summer or a long, cool summer. This measure can not separate the two.

See response to #11.

45. (8) Figure Caption 1 seems to have the author(s) notes or comments inserted into the text.

Fixed

46. (9) perhaps a semantics issue, shouldn't the title read Northern Hardwood Forest, not Hardwoods?

Done.

Ecological Applications: 06-0512

"Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis* (Coleoptera: Scolytinae)"

## Responses to reviewers

31 July 2006

Our thanks to the reviewers and the associate editor for their thoughtful critiques of our manuscript. We have adopted all of the suggestions, including adding the requested experimental details and revising the last paragraphs into a conclusions section. We think that the manuscript has been greatly improved by these revisions and we hope that you will now find it suitable for publication in *Ecological Applications*. Our point-by-point responses to comments are detailed on the following pages.



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Queries/critiques are numbered and in blue Arial font. Responses follow in black Times Roman. Revised prose from within the ms is in red Times Roman.

### Detailed responses to AE

1. You must include more information about the measurement set-up and analytical procedures. Done. See responses #7 and #8 to reviewer #2 (below).

2. The sections headed "Application to management" and "General utility of relating climate, physiology, and population dynamics" should be combined and re-written in the flavor of proper conclusions to the paper. Done.

### Detailed responses to Reviewer 1

1. -the two Y captions confusing in figure 7 (how can the probability of mortality be greater than 1?), We clarified the figure to indicate that the solid lines are probabilities (left-hand axis) and the points and dashed line are in units of average population growth rates (right-hand axis).

2. -the relative changes in temperature a bit obtuse on page 17, line 22, We adjusted the sentence to read as follows. "Based on this regression, average minimum winter air temperature has increased from 1960 to 2004 by 2.8 vs. 5.1 °C in the south vs. north (30.75 vs. 35.75 °N), and by 2.2 vs. 4.2 vs. 4.1 °C from east to west (80 vs. 88 vs. 94 °W)."

3. -the description of the thermal buffering model on page 19, lines 13-16 a bit confusing The sentence now reads as follows. "Regression analyses indicated that thermal buffering ( $B$ ) was greatest in southerly latitudes and when  $K$  was low (see Eq. 7;  $P < 0.0001$  for all coefficients,  $r^2 = 0.63$ , RMSE = 0.88 °C, delta AIC compared to best simpler model = 42,  $n = 840$ )."

4. the description and discussion of the theoretical model of *D. frontalis* population dynamics to temperature on pages 15-16 and page 23 somewhat incomplete. Perhaps it is due to my unfamiliarity with Ungerer et al., 1999, but I read that article, and only after a fair effort was able to puzzle out their methods and significance, I think. The authors may want to review their treatment of this aspect of their work, and modify it if they feel they can make it clearer.

This has been clarified with several changes in the following sentences. "We used this model to evaluate the expected demographic consequences of new information regarding life stage structure and experienced temperatures. Scenario 1 represented baseline knowledge at the start of the present study and so followed Ungerer et al. (1999) in recognizing three life stages (larvae, pupae, and adults) with  $P = 0.379, 0.174, 0.447$ , respectively (based on proportion of total development time at 25 °C in each life stage), and with temperature-survivorship functions ( $M$ ) for each lifestage calculated from empirical frequency distributions of supercooling points: mean  $\pm$  SD =  $-10.5 \pm 2.9, -8.8 \pm 2.6, \text{ and } -11.9 \pm 2.9$  °C, respectively (assuming a normal distribution of supercooling points). Also following Ungerer et al. (1999), the baseline scenario assumed that all beetles experienced a temperature 1 °C warmer than  $T$  to account for thermal buffering within phloem ( $Q_j = 1$  where  $j = T + 1$  and 0 otherwise)."

5. -minimum is mis-spelled on page 31, line 14.  
Fixed. Thanks.

## Detailed responses to Reviewer 2

1. The authors need to expand the abstract to include essential details on the timing and location of the study: when it was done and what time period do the data apply to? Other than saying they used 1439 pairs of site-years, the authors are silent with respect to details of "when and where" with respect to the work

Thanks. Abstract now indicates that studies encompass the southeastern U.S. and that beetle abundance data came from 1987-2005.

2. ... their contention to use temperature to build a model of population dynamics is reasonable. However, they provide no clear rationale for why winter temperature is the key temperature variable. We must infer that if the temperature is low enough, a lot of insect larvae will be killed and thus diminish the next year's population. This is reasonable, but it seems to me that given the sophistication of the rest of the paper some more convincing front-end argument is needed to set up the work. The essential details are supplied as part of the section titled Study System, but it would help to include some details of the reasons in the Introduction.

We added the following sentence (right after the first mention of *D. frontalis*, p5 | 10) to clarify the rationale. "This built on previous studies that have implicated minimum winter temperature as a factor in the survival and northern distribution limits of *D. frontalis* (Ungerer et al. 1999, Lombardero et al. 2000)."

3. Page 6, lines 14-17. The specificity of the claim of the temperature on one winter night in a whole year dropping to -16{degree sign}C somehow defining or "being in concordance" with the northern limit of the southern pine beetle seems too strong a statement to me. I have never heard of such a fine temperature requirement defining an effective spatial limit. I assume it is air temperature that is being referred to. Also, I suggest further explanation of exactly what is meant by the statement "allowing for 1{degree sign}C buffering of temperatures in the phloem.." Does this mean that the minimum can go to -17{degree sign}C?

Ungerer et al. (1999) explicitly justify this statement in their abstract: "Laboratory measurements of lower lethal temperatures and published records of mortality in wild populations indicated that air temperatures of -16° should result in almost 100% mortality of *D. frontalis*. The distribution limits for *D. frontalis* approximate the isoline corresponding to an annual probability of 0.90 of reaching -16 °C. Thus, *D. frontalis* have been found about as far north as they could possibly occur given winter temperature regimes."

We clarified that -16 refers to air temperature and that this was taken to represent -15 C where the beetles live in inner bark. Pg 6, | 20-22 now reads: "... at least one winter night when air temperature dropped below -16 °C (which they judged should result in >90% mortality of the beetle population, allowing for the inner pine bark being 1 °C warmer due to thermal buffering).".

4. Page 7, line 1. Authors need to explain their statement that the data from 50 weather stations in the model "ignored the effects of elevation and microclimate.." Are they suggesting a problem of not adjusting temperature data from the height of measurement in the screen (1.5 m) to some other height, or are they referring to an actual topographic effect on temperature patterns. A similar comment is applicable to their use of the term 'microclimate'.



We clarified as follows: "... were based on only 50 weather stations and ignored altitudinal patterns from adiabatic lapse and microclimatic patterns from thermal buffering within pine trees."

5. Page 8, lines 14-18. Change of point size.

Fixed. Thanks.

6. Page 8, line 21. Authors need to define their use of the term 'lapse rate'. Is it to be taken literally to mean actual or environmental lapse rate or is it a surrogate for a height-dependent weighting coefficient in their interpolation model (equation 1)?

Thanks. Now we call it "adiabatic lapse coefficient".

7. Page 10, starting at line 15. I found the description of the experimental work very brief and quite inadequate for a reader to understand how the authors solved for K, the rate coefficient in the thermal model of the behaviour of tree temperature (their Newton's Law of Cooling). Nine trees were instrumented at five places. There is no mention of depth of measurement of the thermocouples, no mention of age of tree, no mention of height of measurement in the tree, and no discussion of possible affects of other variables such as wind speed that would affect, to some degree, the value of heat loss from the bole.

The following sentence was added to the methods. "On each tree, at 1.5 m height, one sensor was placed in the air 8 - 10 cm from the tree, and the other was inserted through the outer bark via a minimal tangential incision (1 mm diameter) into the thin (1 - 3 mm) phloem layer where *D. frontalis* would occur; the incision was then sealed with a dab of silicone."

We did not age the trees, but presumably size (DBH) is the more relevant metric for thermal buffering. We were unable to measure wind speed, but this must not have large effects on buffering because the models all provided good fits even though wind speed must have varied from place to place and night to night.

8. Page 11, line 21. Authors need to augment the description of the experiments conducted to determine the lethal temperatures. Like my last point, the experimental description of cold tolerance determination leaves out important details. How were the thermocouples attached to the insects? What determined the two cooling rates? By implication, rate does not matter, but reaching crystallization does.

We revised these sentences to include the requested details. "Thermocouples were attached with tape to the surface of individual beetles that were then slowly cooled in an air chamber within a low-temperature water bath. As cooling proceeded, the temperature of each individual beetle was recorded at 1-sec intervals using a 16-channel recorder (THERMES data acquisition system, Physitemp Instruments, Inc., Clifton, New Jersey). The instant when each beetle froze was marked by a conspicuous exotherm from the heat of fusion. Supercooling points were taken as the temperature of the insect immediately preceding the exotherm. Most measurements employed a standard linear cooling rate of  $-0.2\text{ }^{\circ}\text{C} / \text{min}$  (e.g., Lombardero et al. 2000) but we also conducted two trials with a very slow cooling rate of  $-0.04\text{ }^{\circ}\text{C} / \text{min}$  to verify that this experimental detail did not affect supercooling points."

9. Page 12, lines 9 to 17. I find this paragraph quite confusing. In line 9, with respect to the comment on lower lethal temperature, the question is "lower compared to what?".

"Lower lethal temperature" is from the vocabulary of physiological ecology. We adjusted the words so that non-physiologists will understand. "Our studies used supercooling

points as estimates of lower lethal temperature (the temperature below which death occurs). To validate this, ...”

10. Page 12, line 20. Why -15.3{degree sign}C and not -15.6{degree sign}C, one of the supercooling points (see same page line 11).

-15.6 °C was our target, but the actual temperature we attained was -15.3 °C. This was close enough to accomplish the objectives of the study.

11. Either on page 19 or in the caption to Figure 4, authors must tell the reader where the 25 sites are located. Now they only say in the southeastern US, with one outlier in WV. I would suggest some more specific locations would help the interpretation.

This information is in the methods (pg 11, l 18-19). “... 140 historical time series of hourly temperatures during midwinter (1 December to 28 February) that were available for 7 recent years (1998-2005) from 25 NOAA climate stations distributed across 16 states (AL, AR, CT, DE, GA, IL, KY, MD, MS, NC, NJ, PA, SC, TN, VA, and WV) in the region of interest.”

12. Application to management. I did not find that this section added much to the content of the paper. It could easily be deleted or some minor points on the relevance of the findings to management (all minor) could be added to the Conclusions.

13. I found this section unhelpful. It strays into a very general discussion of modelling population dynamics and seems to bear only very marginal relevance to the content of the work reported in the paper. The basic point made is that the model developed for southern pine beetle is general enough to be applied to other species. I believe that such a claim needs further justification that has not been argued convincingly by the authors.

14. The paper would profit from a Conclusion.

For 12-14, see response to AE point #2.

Response to reviewers' comments:

Reviewer 1:

Significant points:

- 1) Line 138: The landings we monitored were naturally occurring. This has been clarified in the sentence.
- 2) The term "scrounger" has been replaced with "late arriver" throughout the MS.
- 3) Lines 38 and 280: "Pre-landing" has been added to both sentences.
- 4) I did not think that the fact that we sampled landing beetles from only two trees was an issue, because at that stage, we were sampling dispersing beetles from many different brood trees that were flying at that time. With boring beetles, we needed to sample beetles from the same tree to eliminate differences due to inter-tree effects, and determine whether individuals differ. To clarify what we did, I have reworded the sentence in the discussion to read "Our results also reveal that pheromones that are directly derived from host precursors (*trans*-verbenol, verbenone, and myrtenol) (Hughes 1973, 1975; Renwick et al. 1976) were detected in much higher amounts than those derived by *de novo* synthesis (frontalin and *endo*-brevicommin) (Vanderwel et al. 1992, Barkawi et al. 2003) in beetles that were dispersing from different trees in the vicinity and landing on the two trees that we sampled, as well as in boring beetles that we excised from one tree".
- 5) Line 227: Fig. 2 that was cited was a typographic error. It has been rectified to (Table 1, Fig. 1 lower).
- 6) Line 286: Pre-landing pheromone production has been added to the sentence.
- 7) The landing insects were captured in traps before they actually landed on the tree, i.e. they landed in the trap that was superimposed on the tree, instead of the tree. The way the experiment was set up, we captured the late arrivers before predators could, and so there was no effect of predation on the experiment itself. I agree however, that predators have a disproportionate effect on late arrivers. I have added a citation to the introduction and a sentence to the paragraph in the discussion that deals with pheromone production and fitness costs in insects.

Minor points:

- 1) Line 113: The citation has been added. "Should" has been changed to "might".
- 2) Our replicates are individual beetles. We had to use beetles from the same tree to minimize effects due to inter-tree variation that would have confounded our study.
- 3) We analysed males and females together to decrease the number of statistical tests performed and have retained it as is.
- 4) Lines 232-245: I agree. I was expecting a tradeoff, but it does not seem to be the case.
- 5) Figures for gallery length have been included in Fig. 2. And the offspring data has been retained as Fig. 3. Corresponding changes in the text have been made.
- 6) Lines 273-278 have been deleted.
- 7) Line 279: "pre-landing" has been added to the sentence.

- 8) Line 336: It was consistent with our main theoretical prediction (last sentence in introduction) that the costs and benefits with being pioneers or late arrivers would equalize fitness differences between them.
- 9) Table 3 has been retained as is.
- 10) Lines 326-7, 330-1, 334-5: I have added relevant information and cited Raffa and Berryman 1983.
- 11) Line 346: "Indicate" has been changed to "are consistent with the view. Line 348: "some of" has been added to the sentence.
- 12) Line 412: *Dendroctonus* has been italicized.

Reviewer 2:

- 1) I performed an ANCOVA to examine the effects of arrival time with gallery length as the independent variable and fitness as the dependent variable. The results were not different from the ANOVA and regression analysis that we reported in the paper.
- 2) The REGW multiple comparisons test is an alias for the Ryan's-Q test. It uses a multiple stage approach that controls maximum experiment-wise error rate under any complete or partial hypothesis. It is the most powerful test for all pairs comparisons and is recommended by Day and Quinn (1989). It is a common procedure used to analyse data in studies of scolytids and their associated insects (Reeve and Strom 2004). I have added this explanation and cited these papers.

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Associate Editor for Forest Science

Thank you for the positive decision letter. I attach a new version of our manuscript 2004-FS-091, "*Mismatch between herbivore behaviour and demographics contributes to scale-dependence of host susceptibility in two pine species*" by Tiina Ylioja, Daniel H. Slone and Matthew P. Ayres in enclosed. We have considered the comments and suggestions of the Associate Editor and the two reviewers.

We agreed with the comments and corrections of our reviewer. In attached rebuttal letter are our detailed responses to the suggestion and indications of following it.

Thank you very much for you co-operation.

Sincerely,

Manuscript 2004-FS-091: our responses to suggestions by Associate Editor and 2 reviewers:

(Comments underlined, our responses with normal font)

### 1) Associate Editor(Comments):

lines 12 - 15 , p. 6

Removed.

The editor could not find Ungerer et al. 1999 in the text.

Ungerer et al. 1999 was in the text on page 3 line 18

p. 1, L5 - I recommend replacing "host organization" with "geographic scale." The former sounds like a group that meets every so often.

Replaced.

p.3 L5-8 - No mention is made of relative host suseptibilities to SPB. Would it be helpful to include such information?

It is difficult to rank the pine species according to their susceptibilities based on literature.

p5. My take on Va pine being a less suitable host has to do with the fact that the resin does not crystallize very fast and beetle brood have difficulty developing under those conditons. Although I can't cite a paper offhand, it would seem to me that this has been documented before. Can you comment on this when you submit your revision?

As this was also pointed out by reviewer #1 we have deleted the end of the sentence.

Lit cited section: Include # of pages for books, not just pages from the chapter.

Total pages numbers added.

Figs, upper and lower is not typically used. Can you change to fig 2a,b, 3a,b, and 4a,b?

Changed accordingly.

### 2) Reviewer #1

1. Title: I suggest changing "explains" to "contributes to". That leaves the door open for future research.

Changed.

2. Pg 2, l 3: I'm ok with calling bark beetles "Scolytidae", but some get quite upset by it. Whichever you prefer

Changed: "Scolytinae".

3. Pg 2, l 23: scales – plural

Changed.

4. Pg 2 l 14: I think "absolute" is a more appropriate word than "intrinsic";

Changed.

5. Pg 3 line 16: This wording makes it sound like beetles aggregate at places other than on trees - reword.

The sentence is changed into:

"The populations of local infestations are started during winter and spring when dispersing beetles employ pheromones to aggregate on individual trees to initiate mass-attacks at points within the forest."

6. Bottom of pg. 4 - Top of Pg. 5: This paper hinges on beetle reproductive rates being lower in Virginia pine than loblolly pine. So that needs to be presented unambiguously to convince your audience. Normalize for beetle attack density and tree size, which affect progeny per attack. This will help the reader understand if it's likely due to resistance, small size, etc. I'd delete "may also be related to oleoresin chemistry" if you don't know.

The figures for 'progeny per attack' were also criticized by the reviewer #3. It appears that the lower reproduction in Virginia pine could be explained by the higher number of attacks (in Virginia than in loblolly). The figures are correctly cited from Veysey et al. 2003 but the fact that the measurements in Veysey et al. 2003 come from two nearby sites makes this confusing. The measures on attack preference of beetles (page 4 line 21-22) come from a site where Virginia and loblolly grew thoroughly intermixed and allowed beetles to show attack preferences. The data on reproduction (page 5, lines 1-2), however, come from a site where the two pine species were not intermixed and grew more or less separated from each other. In that site no differences in attack densities in Virginia and loblolly pine were detected (which lead to the follow-up study of the submitted manuscript). When the values on page 5 lines 1-2 (0.9 and 4.7 progeny per attack) are adjusted for surface area of the bark they are 5.2 and 27.1 progeny per 250cm<sup>2</sup> in Virginia and loblolly, respectively. Veysey et al. 2003 does not provide more detailed information on tree size but states that the 'trees of both species averaged 20-30 cm in diameter, 18-22 m tall, and 25-30 year-old'

"May also be related to oleoresin chemistry" deleted

7. Pg 6 | 8: spelling of Liquidambar;  
Corrected.

8. | 13-15; this doesn't fit in Methods section;  
Removed as suggested by the Associate Editor and Reviewer #3.

9. Figure 4: Restrict age axis to age ranges of trees that southern pine beetle commonly attacks. The youngest trees in the data set are 37 yrs (Table 1). The power of simulation is that you can extrapolate beyond that, so you needn't restrict it to 37+yrs. But even so, make it more biologically realistic by truncating this axis to a reasonable age @20 yrs?

There appears to be misunderstood. The data represented in Table 1 describe only those 5 stands that we sampled (with the help of the GIS-layer that contained the data for the whole National Forest) and were used to verify the result of Virginia pine being more often attacked than loblolly when trees grow intermixed within stands. In contrast, data in Figure 4 include the whole GIS-data that is not simulated, instead the points in the graphs demonstrate actual (but binned) data. The age range is wider than of those stands listed in Table 1. It is known that southern pine beetle only rarely infests stands <20 years old, but during an epidemic the damage can extend peripheral areas like young stands when beetle run out trees of suitable size, and thus we feel that the x-axis describes biologically meaningful age range.

10. Sometimes in the Discussion and Abstract it was not always apparent what was based on simulations vs. actual data, or more precisely when simulations extended beyond the value limits of the available data. That should be clarified.

This is related to the previous point (9). We have not simulated the data in any point beyond the value limits of the available data.

### **3) Reviewer #3:**

The data cited from a previous paper on brood production (Veysey et al. 2003) may be a bit misleading. Brood production from Virginia pine is not as low as it appears

relative to loblolly if it is shown as production per square meter because the low "per attack" production is offset by higher attack densities on Virginia pine.

See comment #6 of reviewer #1

P. 12, L 16 - Insert "of" between mortality & Virginia.  
Corrected.

Abstract, L 8 - "flying beetles" do not attack. They land first.  
"flying" is omitted.

P 6, L 14-15 – irrelevant;  
removed (as suggested also by Associate Editor).



Editorial Board, Forest Ecology and Management

Ref.: Ms. No. FORECO1167. Lombardero et al: "Effects of fire and mechanical wounding on *Pinus resinosa* resin defenses, beetle attacks, and pathogens"

13 November 2005

Thank you for the opportunity to revise our manuscript. Below we summarize our responses to the reviewer's comments. We believe that all of the comments have been addressed in a way that the reviewers would find satisfactory. We thank the reviewers and editor for their detailed and thoughtful critiques. The manuscript has been greatly improved as a result of their efforts.

### Reviewer #1

3/2

The reviewer is correct that some pathogens are remarkably tolerant of resin. We have qualified our statement (copied below), and added references that indicate resin probably is a defense against many pathogens, including the specific fungi relevant to our study system. The relevant sentence in the introduction now reads: "An important primary defense of pine trees against insects and many pathogens is oleoresin, a mixture of monoterpenes and resin acids that flow from physical wounds and provide a chemical and physical barrier against biotic intrusions (Reeve et al., 1995, Franceschi et al., 2005; Hofstetter et al., 2005; Klepzig et al., 2005)." The 4<sup>th</sup> para of discussion now includes: "the monoterpenes in oleoresin have demonstrably negative effects on the growth of *O. minus* on agar medium (Hofstetter et al., 2005)"

3/24 Done

#### Materials and methods

We have revised the methods, especially "Overview of experiment" to clarify the design. We could also add a diagram upon request, but we think the text is now sufficiently clear and we already have 6 figures.

6/10-13

This is now clarified in the methods under "Fire".

6/21 Done

7/1-9

We clarified this in the methods under "Mechanical wounding".

7/11 Done

7/12-22

This has been clarified in the methods under "Attraction of bark beetles to burned and wounded trees". Trees were randomly chosen from within all treatment combinations. The text now indicates that sticky traps were located at 1.5 m height, that resin measurements were made at 100-120 cm height and that wounds were 30 cm above and below. Therefore sticky traps were located above the highest wound and resin from the wounds did not interfere with trap function. The text now indicates that we used pheromones to attract beetles to the site with our experimental trees (else we would have had too few beetle landings to test for treatment

effects). We could not affirm ahead of time that pheromones would trump all other attractants. In fact, neither fire nor wounding treatments affected landing rates, but fire increased the probability of attacks given landing. This was the first experimental test for effects of scorching on tree-specific landings and attacks in interspersed pine trees.

8/4-6

The text now indicates that the outer bark of the tree was partially shaved to facilitate penetration of the metal punch, and subsequent inoculation. As indicated, the punch was 3 mm diameter, which we inoculated with a 1 mm diameter plug of actively growing fungus. Lesion measurements included the 3 mm perforation, which was trivial compared to the lesions themselves.

8/16 Done

9/8 Done

10/10 Done

10/12

The text states that “burned trees on average had resin flow that was lower, but insignificantly so, compared to that of unburned trees ( $F_{1, 28} = 2.39, P = 0.13$ )”.

11/10-5

We have added a B&W image as Fig 4 that shows what we describe here and also shows the pattern of beetles attacks within the scorched area, which we describe later.

11/18-24

See our response to 7/12-22. There are many examples of bark beetles responding to pheromones plus other volatiles signals differently than to pheromones by themselves. Without doing the study, we could not know whether or not beetles would be more likely to land on trees that had a pheromone signal plus scorching vs. the pheromone signal by itself. It is only with the combination of landing data and attack data that we know the effect was due to post-landing discrimination. Thus, we have retained the landing data in the results.

12/6-8 As requested, we have added a B&W photograph that shows what we describe here (as new Fig. 4).

12/21-23

Inspection of the cross sections revealed an obvious positive correlation between lesion length and depth, but no measurements were made. Accordingly we state in 13/9 that “longer lesions penetrated deeper into the xylem”, but do not have statistical support for a stronger statement. Measuring more lesions on more trees would have required destructive sampling on trees that we wished to continue monitoring.

12/23 - 13/1

The reviewer’s point is fair, but we should not reject oleoresin as a defense against pathogens because monoterpenes are known retard the growth of some fungal pathogens of pine, including one of our study species. We have added the following sentence to the 3rd para of discussion:

“It remains an open question the extent to which preformed resin functions as a defense of *P. resinosa* against pathogens. In our study, there was no correlation between tree-specific resin

flow and the size of fungal lesions. However, the monoterpenes in oleoresin have demonstrably negative effects on the growth of *O. minus* on agar medium (Hofstetter et al., 2005), and it seems probable that the persistent oleoresin sheath that formed over exposed wounds in our study trees helped to protect from infections of the otherwise exposed inner bark during the days, months, and years following wounding.”

#### Discussion

The reviewer is correct that traumatic resin ducts could be part of the responses that we observed. The 1<sup>st</sup> para of discussion now includes the following revision.

“Under this model, any of the experimental disturbances induced biosynthesis of oleoresin. A simple mechanism invokes increased biosynthesis of oleoresin in the existing epithelial cells that line vertical resin ducts, followed by secretion into the vertical resin ducts where resin could be conducted via lateral ducts to new points of wounding (Lorio, 1993). However, we were unable to test for the de novo formation of traumatic resin ducts, which can contribute to systemic resin flow and which are known to be produced in some conifers following wounding and/or inoculation by pathogens (Nagui et al., 2000; Franceschi et al., 2005; Luchi et al., 2005).”

14/4-7

We have adjusted the 2<sup>nd</sup> para of discussion as suggested and added context from a recent review of conifer defense systems (Franceschi et al., 2005).

15/4 Done. We have replaced “attractiveness” with “acceptability” (as suggested by reviewer #2).

15/8-9. See earlier responses regarding pheromones.

15/17 Done

16/3-6

1. We monitored these trees periodically, and we know that the attacks happened during the first week
2. We agree with the reviewer. The text states “the trauma of the disturbance somehow interferes with resin flow during the following days (Blanche et al., 1985) and creates a window of opportunity for successful attack by even small numbers of beetles.” We portray the short-term decline in resin as due to a physiological perturbation in the tree and not an evolved response to the beetles. We hypothesize that the attraction of beetles to scorched trees is an adaptation that exploits compromised defenses in disturbed trees. We also hypothesize that the subsequent increase in resin flow beyond baseline levels is a counter-adaptation of the trees to the increased risk of having attracted beetles immediately following the disturbance. We have retained the hypothesis of fire-mediated coevolution in the last paragraph of the discussion. It should be clear that this is a hypothesis for provisional consideration and further testing, rather than a conclusion that should be unequivocally accepted.

16/9 It is “facultative” in the usual sense that inducible defenses are facultative changes in phenotype following a stimuli that portends increased risk of future attacks.

#### Figure legends

1. We have retained Fig. 4 as rationalized above.
2. Done
3. Done

4. Done
5. Done
6. Done

## Reviewer #2

3/17 Done

4/2 Done

4/11. We acknowledge that resin in other parts of the tree may be different. From 1<sup>st</sup> para of discussion: "Our study was restricted to measurements of resin flow from the lower bole, which is relevant to interactions between *P. resinosa*, surface fires, and *Ips* bark beetles (Santoro et al., 2001), but we cannot infer anything about responses of the resin system higher in the bole of our study trees (Tisdale and Nebeker, 1992).

8/4 Done

Fig. 1& 2 Done

Fig. 4 & 5 Done

Fig. 6 Done

13/20 Done

14/7 Done

14/14 Done

14/22 Done in the text

15/4 Done

15/17 As suggested, we have removed the word "attracted" here and now say that "bark beetles are more likely to attack scorched trees".

16/3 In our experiment we carry out a quite artificial fire, but it was the only way to have our experimental trees intermixed. We did not expect successful colonization as happens in nature, because the burned area was small and quite different to real surface fires. But literature is full of evidences that *Ips* bark beetles successfully colonize trees after fire, and Santoro et al. (2001) presented evidences that *Ips* species may kill red pine in the area.

16/3. As requested, we have added further description of *Ips* biology, particularly the point of whether they kill trees. The 2<sup>nd</sup> para of Intro now says: "*Ips* are often considered secondary colonizers of dying trees rather than primary agents of tree mortality (Rudinsky, 1962 ; Paine et al., 1997 ), but there are also frequent reports of *Ips* killing trees (Schenk and Benjamin, 1969; Sartwell et al., 1971; Geiszler et al., 1984; Goulding et al., 1988; Rasmussen et al., 1996; Kegley et al., 1997; Hammond, 2004; USDA Forest Service, 2004). Santoro et al. (2001) found that *P. resinosa* being attacked by *Ips* (and frequently dying) had been growing as fast as

nearby unattacked trees prior to the attacks, implying that they were otherwise healthy and would have likely lived had they not been attacked.”

16/8 Done

Dear Dr. Lombardero,

Thank you very much for submitting your manuscript "Evaluation of the enemy release hypothesis for pine forestry in Spain" (Article) for review by *Ecological Applications*. The reviewers and I appreciate the work you have accomplished. Based on the reviews, we are willing to consider a revised version for publication in the journal, assuming that you are able to modify the manuscript according to the recommendations.

Both reviewers have major reservations about the manuscript, but they differ considerably in their specific concerns. Reviewer 1 has indicated a number of issues that need clarification, and feels that the manuscript, as written, may be more appropriate for a forestry journal. Reviewer 2 has one primary concern, which is that the study does not really examine the enemy release hypothesis. Although the reviewers do have substantial concerns about the manuscript, the study does have some very interesting aspects, and I feel that there is potential for a revision to bring the manuscript to a level that would be appropriate for *Ecological Applications*. Both reviewers have provided comments that can provide direction for substantially improving the manuscript and that need to be fully addressed in the revision. I have carefully examined the manuscript and find all of their points of merit. Overall a major revision of the manuscript is necessary. Below I provide some further comments about the manuscript and reiterate some of the reviewer's comments that I find especially important.

The major concern of Reviewer 2 about the appropriateness of the study for testing the enemy release hypothesis needs careful consideration. I agree with the reviewer that the hypothesis relates to increased growth (fitness) of a plant in an introduced range as result of release from enemies in its native range, and does not address the effects of enemies native to the introduced range. These are related ideas, but they are not the same, and the distinction between them is important. Thus I agree with the reviewer that your study does not actually examine the enemy release hypothesis. However, the study does address interesting questions about introduced species in relation to native enemies. Thus a major rewrite of large parts of the manuscript seems necessary to clarify the relationship of the work to ideas about introduced species. A change in the title also appears appropriate. Reviewer 1 also suggests changing the title.

The Introduction is mostly good but will require substantial changes to more appropriately set the context of the study in terms of ideas about introduced species. Also, for the first paragraph of the Introduction consider the recent ideas for *Ecological Applications* (Please see the editorial in the Feb. 2006 issue.).

Reviewer 1 has some major concerns about the Methods section. Confusion about plot and stand is especially important. I assume there was one plot per stand, but this is not clear. If so, use one term for the sampling unit throughout the manuscript. In addition, a little information about the plots would be good, such as size, number of trees, and criteria for location within a stand. On line 183 (p. 9) it would be helpful to know how many trees were in the plots in order to have some idea of the sample sizes for number of infected trees. More needs to be said about the fungal attack (perhaps this should be in the Introduction), and it would be nice to know if the fungus is native.

The Results section needs some attention. Figures 4 and 5 need more complete explanation in the legends (comment of Reviewer 1), and the text about these figures could use some clarification. The use of plots and stands is confusing in this context.

The Discussion needs substantial revision, especially to clearly set the work in the context of ideas about introduced species and the enemy release hypothesis. I think that the Discussion could be reduced somewhat in length, as also implied by Reviewer 2. For example, the two paragraphs on lines 292-322 could be tightened some.

Addressing the above issues and other comments of the reviewers will require considerable effort, but should notably improve the effectiveness of your paper. This is an interesting topic, and your work has the potential to yield a good paper. I look forward to seeing your revision.

Your revisions should address the specific points made by each reviewer. You should also send a cover letter, indicating your response to the review comments and the changes you have made in the manuscript. If you disagree with a reviewer's point, please explain why. Use the link below to submit the revised version.

Sincerely,

Subject Matter Editor  
Journals of the Ecological Society of America

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Reviewer #1 (Other Suggested Journals):

Journal of Forestry, Forest Science

Reviewer #1 (Comments to Author):

The ms. reports a side-by-side evaluation of native bark beetle attack on native *P. pinaster* and introduced *P. radiata* in plantations in Spain as a test of the ERH. If the goal of the authors was to provide information for forestry in Spain, the title provided is appropriate. But I think as a title for an ecological journal, especially where the ms.'s stated goal is to examine ERH, the current title is too restrictive. I suggest it be recast to address ERH in broad terms.

Field evaluation of the ERH is generally appropriate and the general experimental design (once confusion on the term "plot" is clarified, see below), seems appropriate.

Much hinges here (e.g. independent axis in Fig. 2 and the conclusions derived from Fig. 2) on knowing that the lumber yard was indeed the source of the bark beetle (see lines 140-142 and line 153). Was any sampling for bark beetles conducted in the lumber yard itself to confirm this point? Are there any other sources for these beetles in the vicinity of the plantations and how far away are they?

An unfortunate omission in the explanation of what is a "plot" in the Methods section (p. 8, line 157) plagues clarity of the ms. from that point onward. Based on the caption in Fig. 1, the reader can deduce that "plots" refer to the 45 stands in which trees were measured. This section must be re-written so that there is no ambiguity about the experimental unit is being discussed here.

Fungal attack is introduced abruptly in the Methods (no mention of it in the Introduction). That omission needs to be addressed as well as whether it is known if *S. sapinea* is a native fungus

in Spain. Admittedly, determining the native geogr. range of fungi is problematic but would allow placement of the native beetle and the fungus in their correct context.

p. 8, line 164. How were the main branches selected? Same question for branches measured in line 193.

Lines 197-200. I do not understand the rationale for measuring shoot size for shoots that had fallen from trees, presumably the result of *T. piniperda* damage.

p. 16, line 332-334. No quantification is provided to back up the statement on the stout needles of *P. pinaster* compared with the long needles of *P. radiata*. This is a very important omission as the greater loss of PS tissue in *P. radiata* compared with *P. pinaster* is central to the argument here that the ERH is only operating with respect to some parameters (% trees attacked) but not others (extent of damage to each tree).

Figs, 4 & 5 cannot be critically evaluated as neither has explanation as to the apparent error terms about the means for diameter, height of trees in the plantations. Are these SE? SD? Other?

Minor point: to use "debunk" in the abstract is too strong a term here; the ms. does not debunk ERH, it merely provides information on conditions in which it operates and to what extent.

Although these results do not substantially alter our view of the ERH, they do provide a reminder that the hypothesis needs to be evaluated from different parameters of plant performance and that escape from one biological agent does not mean of course the introduced plant has escaped attack from others (e.g. the fungus in this case).

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Reviewer #2 (Comments to Author):

Biological invasions are commonplace world-wide. Some nonindigenous species (NIS) perform exceptionally well in new habitats, displacing or reducing abundances of native species and altering ecosystem properties. One hypothesis that may account for enhanced performance of the NIS in novel ecosystems is the enemy release hypothesis. This study addresses an applied aspect of the enemy release hypothesis as it relates to performance of introduced *Pinus radiata* relative to that of native *Pinus pinaster* in Spain. The study is comprehensive and interesting, the results appear to be appropriately analyzed and interpreted, and the writing is quite good although the discussion is somewhat wordy. I was particularly impressed that the authors did not simply count attacking herbivore species and/or pathogens to illustrate enemy release, but rather used fitness metrics that clearly would be affected by herbivores and/or pathogens and are illustrative of species responses to attacking species. The figures are informative and well prepared.

The only major shortcoming of the paper that the authors need to address up front is this: they appear to define the enemy release hypothesis (ERH) differently than it is commonly and historically used, and, since this definition framed their entire study, I am not convinced that what we are looking at here is enemy release at all. I have checked with a number of sources (Keane & Crawley 2002, TREE; Wolfe 2002, Am. Nat.; Colautti et al. 2004, Ecol. Lett.; Agrawal



et al. 2005, Ecol.; Blumenthal 2005 Science, 2006 Ecol. Lett.) for their interpretation of what constitutes ERH. All of the aforementioned papers refers to loss of native enemies by NIS in introduced ranges. As it is used in this paper, ERH refers to performance differences between native and introduced pines based upon attacks and infection by (apparently) species that are native to the introduced range. Thus, there is no measure of faunal reduction from the native range of the NIS in its introduced location(s).

Despite this concern, the paper is interesting because while attack rates are consistent with lower attack rates on the NIS than the native pine, the matter of importance - fitness consequences of attacks - are greater for the NIS than for the native species. While the finding that attack rates are higher near timber yards may be known by specialists in the field, I think may Ecol. Applic. readers will find the results interesting nevertheless. As well, the apparent interaction between attacks by *Sphaeropsis* and *Tomicus* lends support to the concept of multiple or synergistic/additive stressors.

The overall findings that radiate pine may incur greater losses to attackers is interesting in light of the frequency with which the species is planted around the world in silviculture. The authors attribute this to knowledge by the tree planters that enemy release may work in their favour, although another more plausible, in my view - hypothesis would attribute this pattern to herd mentality. If the author are aware of documentation that supports tree plantations to minimize losses to enemies, they should provide it.

#### Specific Comments:

line 26: or because of previous commercial experience? e.g. copycat planting

line 62: insert: 'are assumed to' in between they and have

line 82: could the NIS be adapted to the enemy if they did not coevolve?

lines 123-124, 128: references?

lines 326-327: Can you review literature to demonstrate whether the ERH is or is not supported in silviculture around the world? The species is sufficiently well planted, we should be able to discern if it fact this species experiences true release from enemies.

line 409-418: you need references for many of the points made in here, as it seems anecdotal as it is presented.

line 420-421: examples of this are numerous e.g. Eucalyptus in different countries introduced with or without herbivores (described in Elton's book).

#### Reviewer #2 (Other Journal(s)):

Biol. Invas.; Diversity and Distributions?

Please note: this decision letter is blind-copied to the referees.

May 5, 2006

Dr. Matthew Ayres  
Department of Biological Sciences  
Dartmouth College  
6044 Gilman  
Hanover, NH 03755-3576  
United States

Dear Dr. Ayres:

Re: Manuscript No. 06-12 - Climatic effects on caterpillar fluctuations  
in northern hardwoods forests by Lindsay V Reynolds, Matthew P. Ayres,  
Thomas G. Siccama, and Richard T Holmes

The above-noted manuscript may be acceptable for publication in the  
Canadian Journal of Forest Research after major revisions. In your  
revisions please pay careful attention to the attached comments of the  
referees and the Associate Editor. The revised manuscript will be  
carefully evaluated by the Associate Editor.

When you submit the revised manuscript, please include a cover letter,  
in which you quote the manuscript number, itemize each comment of the  
referees and the Associate Editor, describe in detail (with reference to  
page and line number in the revised manuscript) how you have addressed  
each of their comments in the revisions, and respond to those comments  
with which you disagree.

Sincerely,

Co-editor, Canadian Journal of Forest Research

## Associate Editor's Comments on Manuscript #06-12

### **Climatic effects on caterpillar fluctuations in northern hardwoods forests by Lindsay V Reynolds, Matthew P. Ayres, Thomas G. Siccama, and Richard T Holmes**

This paper explores the relationships between population fluctuations of forest caterpillars and climate over a 20-year period in the White Mountains, New Hampshire. Caterpillar biomass was the principal variable investigated, and was based on the pooled data for all caterpillars collected during each sampling period. This paper was reviewed by three entomologists who all have solid experience in caterpillar population dynamics, and responses to climatic events. All three reviewers felt the paper may be acceptable to CJFR after proper revision, but all three raised important questions that the authors need to address. A brief summary of the reviewers' comments follows. In addition to several valuable editorial suggestions, Reviewer 1 (a) asked if the lepidopteran population fluctuations could have been caused by just one or a few outbreaking species, (b) suggested some alternative analyses and wondered about the statistical power of some of the tests that were employed, (c) suggested a figure showing the relationship between winter temperatures and caterpillar survival, and (d) questioned whether univoltine lepidopterans are ever "time stressed" especially if they are spring feeders.

Reviewer 2 raised a series of concerns, including (a) lumping all lepidopteran species as simply "caterpillars" and asked if separate analyses could have been done for the most commonly collected families (e.g., Geometridae and Noctuidae), (b) analyzing the "lowest minimum daily temperature" as the most extreme weather event affecting insect survival, rather than perhaps the lowest 5-7 day running average of minimum daily temperatures, (c) considering the entire period October-April as the "overwintering period" rather than analyzing separately the coldest periods during the three seasons of fall, winter, and spring, and (d) the statistical approach used for the time series analyses and the tree-ring analyses.

Reviewer 3 was also concerned about the possibility of a few outbreaking species having had a major influence on the "caterpillar biomass" variable given that all lepidopteran species were pooled. Was any attempt ever made to identify the larvae to family, genus, or species? Were any notes taken on the occurrence of outbreaking species or the lack thereof during the 20 year period? Can any of the analyses be done for just the most commonly collected families, genera, or species? Or alternatively can any of the analyses be done after removing the outbreaking species? Reviewer 3 also questioned (a) if lepidopteran numbers on understory trees is always a good indicator of caterpillar numbers in the canopy, (b) if the caterpillar biomass data could be analyzed separately in terms of spring feeders (the first two sampling dates) and summer feeders (the last two sampling dates), (c) if extreme cold events in spring might be more important to insect survival than during winter, (d) if the possible effects of time lags could be analyzed, and (e) the value of using tree ring growth as a surrogate for tree

1 06-12-AE

chemistry. This reviewer also pointed out that this study did not measure natural enemy levels or the length of the summer season, and therefore care must be taken when addressing these topics in the paper.

In consideration of the above comments, I feel that this paper may be acceptable after revision. The authors should address several of the points raised by the reviewers, attempt some of the alternative analyses suggested by the reviewers, and give special attention to the occurrence of outbreaking species during the study period. Considering that the revised paper may be far different from the current paper, it may be useful to have at least one of the current 3 reviewers look at the next version.

In addition, I would like the authors to add more details as to how caterpillars were searched for and collected. They say that at each sampling point, 100 leaves on sugar maple saplings and 100 leaves on beech saplings were examined for caterpillars. How exactly was this done? How were the saplings selected? Could all 100 leaves have been from a single sapling, from 3 trees, from 100 trees? How were the leaves collected to ensure that the caterpillars did not drop off the selected leaves prior to examination? Did you sample the same saplings on each visit? How did you keep from biasing your search, in that it would be easy to collect only leaves with feeding damage? Were the leaves removed during inspection, or just looked at and left intact? Was the same approach used for all 20 years? Do you have any hard evidence to show that caterpillar numbers on the saplings was similar to the numbers in the canopy foliage? Were they the same lepidopteran species too? On page 5, the authors suggest that the data collected in the present study was primarily to support a bird study (of the black-throated blue warbler), and was not primarily focused on insects. Therefore, I feel the authors need to provide enough entomological detail to show that this paper is sufficiently robust to stand on its own merits as an insect paper.

Also, most weather recording stations are in open fields. Since you sampled insects in the forest understory, wouldn't the air temperatures experienced at such locations have been much cooler, especially during summer? Do you have any temperature data to show how closely the interior forest sites that you sampled matched the data at the HBEF headquarters?

I'd also like to ask how much annual variation occurred in degree-day accumulation at the start of your sampling. That is, you say that you started to sample on June 1<sup>st</sup> each year, and then at 2-wk intervals thereafter. Since insects are cold-blooded, development would be delayed in a cold year and accelerated in a warm year. So, in theory, for the exact same number and species of larvae, biomass would likely be lower in a cold year and higher in a warm year. Can you prepare a figure that shows how many degree days were accumulated by June 1 and July 1 by year during your study period of 1986-2005? Is there any relationship between caterpillar biomass and heat sums as of June 1?

**Referee #1:**

Review of Canadian Journal of Forest Research ms # 06\_12

**Climatic effects on caterpillar fluctuations in northern hardwoods forests**

by L. V. Reynolds et al.

***I do NOT wish to remain anonymous.***

**Comments to the authors**

Name and email of reviewer deleted by MPA.

The question of the role of weather in insect population dynamics is definitely of central importance for much of ecology. However, with the exception of some extreme/ special cases this question has not received sufficient attention, and we actually know very little. This MS is a nice and valuable contribution to this field. The main problem is low statistical power of some of the analyses but this appears to be unavoidable at the present stage. In the following, I will make some comments that the authors may wish to consider when revising their MS.

p 2 | 5 and p 3 | 23 - accelerated insect development due to high temperatures does not usually lead to increased fecundity, you properly discuss this below but I think you should avoid creating a wrong impression also here.

p 2 | 7 - make it clear that you did not test for increased survival, fecundity etc.

p 2 | 17 and p 12 | 3. I do not exactly understand "broad driver" (what would be the opposite, a narrow driver?) - I admit that this may be due to my poor knowledge of English but may you still consider a more explicit formulation?

p 3. I would also mention that the ranges of many Lepidopterans readily respond to climatic changes (like global warming), we see it but do not understand why.

General. I understand that you did not identify your larvae. However, might it have been the case that some peak values were created by one single outbreaking species, *Alsophila pometaria*, for example? Possible confounding effects of such scenario should be discussed.

General. I understand that your time series are not long enough to facilitate the application of proper time series analyses. However, may it still be possible to somehow consider internal (i.e. top-down driven, in the present context) dynamics of insect populations? What about including the density of the previous year in your analyses? I perfectly understand that to calculate correlations between initial values and increments is statistically flawed and density-dependence cannot be studied in this way. However, I have always been wondering if we can include initial values as covariates when studying the dependence of the increments on something else, i.e. would the initial values function as proper covariates even if the tests associated with the initial values themselves would be wrong (if you know the answer, might you consider e-mailing me :-)). In any case, I would welcome a short discussion of possible consequences of ignoring autocorrelations in moths densities in this paper. What about two-way analyses etc, why not to include winter and summer temperatures in a single model?

General. I do not know much about trees and I do not know anything about forestry but I would guess that patterns of spatial autocorrelations in tree growth rates should be well known in general? If this is the case, then why to put so much effort in studying this question here?

P 4 | 25. Any idea about the number of sp involved?

p 6 | 16. lowercase americana.

p 6 , tree cores. Remind shortly why was all this done, the reader has likely forgotten the respective sentence in the introduction by now. Also remind p 7 l 23 what was the rationale of the statistical analysis, what were you looking for? Moreover, may the presentation of the tree core stuff be too detailed? I try to follow the guideline that the amount of text allocated to a question should be roughly proportional to the importance of the question, now I see a slight imbalance here (also in Discussion, but I also understand that this is a forestry journal!), e.g. is it really necessary that the reader knows the magnification of your lense (p 7 l 4)?

Results, beginning. Can you report your total sample size in terms of absolute numbers of individuals? Just to achieve better visualisation.

p 8 l 2. As the effect of winter temperature on moth survival is likely non-linear, I would like to see a graphical presentation of the relationship. Moreover, if the  $r=-0.21$  were the true value, it would likely be ecologically meaningful, so I think you should avoid a too clear-cut no-effect-judgement, and it would be appropriate to complain about low statistical power here.

p 8 l 3. be consistent in presentation: if you report  $r$  for winter temperature, do not report  $r$ -square for summer, just to make the values easier to compare.

p 8 l 8. here and elsewhere (Table 1, Fig.2) - I would definitely understand "growth rate of caterpillars" as referring to individual growth, say this in a different way.

p 8 l 11-12. May comparing tree species be irrelevant here?

p 8 l 19-22. Any analysis of statistical power is always very welcome but I am afraid that the way you do it here is not particularly informative. Would you be able to give e.g. confidence limits to  $cv$ ?

p 9 l 7. "results are unusual" sounds strange. First, rather is this your approach that is original than your results, and, second, - admitting that this may fully be the consequence of my poor English - "unusual" sounds too negative for me. May "original" or "unique" sound better?

p 9 l 10\_15. Here I disagree. A normal univoltine herbivorous lepidopteran is never time\_stressed in our latitudes, reaching the overwintering stage is never a problem. This especially clear for spring feeders like *A. pomonaria* that you mention here which pupates in early May in Maryland, and should be ready at least by early June in your area. You may see e.g.

Tammaru, T., Ruohomäki, K. & Saloniemi, I. 1999. Within\_season variability of pupal period in the autumnal moth: a bet\_hedging strategy? \_ Ecology, 80:1666\_1677.

Tammaru, T., Tanhuanpää, M., Ruohomäki, K. & Vanatoa, A. 2001. Autumnal moth \_ why autumnal? \_ Ecological Entomology, 26: 646\_654

even if I understand that this is not so relevant here but just happy to advertise :\_).

Moreover, there are definitely many sp that are facultatively bivoltine in your area, so "might" is far too soft. For those spp, indeed, reaching the right stage before winter is crucial.

Table 2. I am in a holy war against excessive numerical accuracy, e.g. in  $P=0.1406$  at least the two last digits represent nothing more than numerical noise.

Fig 1. Some internal communication between the authors was forgotten to be deleted. All figures. What was the data point used for calculation of SE in each case? Could this be said in the legend shortly enough?

**Referee #2:**

Comments on "Climatic effects on caterpillar fluctuations in northern hardwoods forests" MS #06-12 by Reynolds et al. for Canadian Journal of Forest Research

This paper investigates possible effects of climatic and host tree factors on fluctuations in abundance of Lepidoptera larvae in hardwoods forests in New England. It uses a correlational approach, which is always suspect according to the old maxim regarding causation. Nevertheless, the authors found one significant set of correlations and provided an appropriate discussion of factors and pitfalls in the analyses. The manuscript is generally well written and clearly organized. I have several comments and suggestions on the methods and analysis.

p. 4, "Caterpillar abundance": I am a bit bothered by the lumping of Lepidoptera species as just "caterpillars". Clearly, different insect species have characteristic population dynamics based on individual species ecology. Given the small sample sizes you were working with, I can understand that you could not investigate individual species patterns.

However, if most of the species were Noctuids or Geometrids, I would rather see you analyze the time series for those families separately. Your perspective seems to be more ornithological (i.e., caterpillars as bird food) than entomological.

p. 5, "Climate data": I do not agree with your choice of the lowest minimum daily temperature to represent overall overwintering mortality.

The temperature on one day seems a bit too random to characterize such a seasonal phenomenon. I suggest more of an aggregative measure of the effects of low temperatures, for example, a lowest 5-7 day running average of minimum daily temperatures. Longer cold periods are more likely to be relevant to insect mortality than is one 24-hour "snap". Alternatively, you might consider a seasonal accumulation of degree days below some threshold temperature, similar to your degree day sums during the growing season.

Moreover, the "overwintering" period considered (October-April) takes in a lot of insect physiology that includes at least three states: pre-diapause, diapause, and post-diapause. Cold periods in the fall or spring when insects are entering or leaving diapause may have greater effects on mortality than do much colder ones in mid-winter when the insect is protected by its full diapause physiology. Thus, you might consider three winter variables, essentially some measures of lowest temperatures in fall, winter, and spring.

p. 5, Methods (for caterpillar time series): From the standpoint of time series analysis, correlations using just the population numbers or population increase rates are not really appropriate. Insect population dynamics are usually characterized as "autoregressive processes", in which density at time  $t$  is influenced by densities at times  $t-1$  and (often)  $t-2$ .

(That is, they are first or second order autoregressive processes. See Royama (1992) *Analytical Population Dynamics* for more on this.) In looking at the effects of climatic variables on population dynamics, you need to run correlations on the residuals of the insect time series, after the autoregressive population processes have been filtered out. These residuals approximate the "random" components of the dynamics—that is, perhaps the effects of weather. The methods for such an analysis are described in Miller et al. (1989) *Environmental Entomology* 18: 646-650.

You can use time series procedures in SAS (PROC ARIMA) to compute the autoregressive models.

You used a similar idea in your analysis of the tree ring data.

However, I would suggest running an ARIMA analysis of those data as well.

If they are fit by autoregressive models, I would use those models to compute residuals for the sake of consistency.

p. 5, l. 8-9 and Table 1. Are the results presented in Table 1 only from HBEF? If so, I would mention this in the table caption.

p.7, l. 23: At the highest abundances, you found less than one half of a gram of caterpillars in a sample of 8,000 leaves collected over the growing season. Is this correct? This seems like an incredibly low number.

p. 8, l. 6-8. I am not especially surprised by lack of correlation between insect population growth and tree ring growth. Any connection between tree ring width and the quality of leaves as caterpillar food is tenuous at best. Moreover, defoliating insects as a rule seem to be less affected by host tree physiology than are insects like wood borers. In addition, defoliators—especially caterpillars—are mobile and can easily choose the leaves they wish to eat.

p. 12, l. 24. This acknowledgement should read "U.S. Department of Agriculture, Forest Service, ..."

Fig. 1. Can you show the time series for the other three locations? It would be useful for the reader to see them as well.



### **Referee #3:**

These are my general/specific comments:

Review of CJFR 06-12

Climatic Effects on Caterpillar Fluctuations in Northern Hardwood Forests

This paper focuses on population fluctuations of the community of lepidopteran larvae found in sugar maple – beech dominated northeastern US forests. Interannual fluctuations in the abundance of caterpillars, the dominant herbivore in non-tropical forests, is of great interest to both resource managers and ecologists alike. I think CJFR readers will find this paper interesting and novel.

In general, this is a well written paper that contributes new information to our understanding of regional dynamics in forest insect populations. In addition, it challenges some long-held, although poorly supported, ideas about the major factors underlying fluctuations in insect abundance.

I do have some criticisms that may be fairly significant if the authors lack the data necessary to deal with them, especially the criticisms in #1 below.

(1) Pooling of all caterpillars in the biomass estimate. The authors use a single measure, caterpillar biomass, as the dependent variable in all of their analyses. This variable was determined for a site (4 in total) from samples collected from leaves at ten points along each of 4 transects. I have several issues with this variable and think that its use in this paper may obscure interesting patterns, or most critically, could in fact lead to erroneous conclusions about population fluctuations.

First, this variable is a composite of many different species collected over a 2 month period each summer. While a large number of species may be part of this measurement, the majority of the biomass is probably attributable to a relatively small number of species. Thus the relationships found are really reflecting the population dynamics of a few dominant species rather than the lepidopteran community as a whole. I'd like to see a breakdown of the proportion that each species contributes (especially those that are abundant). Secondly, and most critically in my opinion, is the potential influence of outbreak species on the overall patterns of abundance. The cycles of an outbreak species such as forest tent caterpillar, cankerworms, or saddled prominent could contribute a large portion of the biomass in years when they are abundant. Thus apparent fluctuations in lepidopteran larvae as a composite may simply be reflecting the contribution to the biomass measure made by the rise and fall of outbreak species. I note that forest tent caterpillar has been very abundant in the northeast US (including, I believe, the area in which this study was conducted) during the time period with the highest biomass and again 10 years earlier (see Fig. 1). If outbreak species were important in these collections and were pooled with the other caterpillars in the composite of biomass, I suggest that they should be removed and the analysis done separately.

In Butler and Strazanac's (2000) Lepidoptera sampling paper, they found that most of the species diversity was in the families Geometridae and Noctuidae (as the authors of this paper also suggested, Page 4, line 24). However, 57% of the total numbers of larvae in the Butler and Strazanac study were gypsy moths. In this manuscript, we are not given a sense of what proportion of the biomass is composed of what species.

Another potentially confounding factor is that some species may increase when outbreak species become abundant. The mechanism behind this pattern is not clear although release from natural enemy pressure because of the abundance of alternative prey (the outbreak species) is one possibility. Lastly, although the authors suggest that caterpillar abundance on undergrowth trees reflects abundance in the canopy, this may not always be true. For example, light to moderate defoliation of the canopy by an outbreak species may force caterpillars of other species down onto the undergrowth trees giving the illusion of densities that are much higher than in other years when the canopy is intact.

My main point here is that the presence of one or more outbreak species can have an enormous influence on the pooled estimate of caterpillar biomass. It is critical that the authors document whether fluctuations in the density of outbreak species occurred during the duration of the study. If so, my preference would be separate analyses to remove the contribution of these species. If the authors can not do this (because species identities were not recorded in some or all years), I feel that the utility of this paper will be diminished considerably. Of course, if outbreak species were not important over the duration of the study (and the authors should state this if true), then much of the criticism above will not be valid. The authors need to be much clearer about how the caterpillar data was collected and what the nature of the data is.

(2) Pooling of temporal guilds. Lepidoptera in northern temperate forests can be broadly grouped into two temporal guilds, spring and summer feeders. In the analysis of summer temperature, this paper pools four sampling dates (in June and July) into an aggregate measure of Lepidoptera abundance and uses this as the dependent variable. However, this may greatly reduce sensitivity. Although the paper indicates a significant correlation between thermal accumulation and caterpillar biomass, it would be more informative to look separately at these two temporal guilds. Spring feeders are generally regarded to be more influenced by annual variations in temperature than summer feeders (see A.F. Hunter 1991, 1995). Thus, looking at temperature differences across an entire summer on all Lepidoptera may miss critical time periods, such as the first 3 or 4 weeks after bud break which may determine the success or failure of many species in the spring feeding guild. The results of Raimondo et al. 2004 suggest a strong correlation between population densities of Lepidoptera sharing the same seasonal time period irrespective of feeding habit and host species. Spring-feeding species are often severely constrained to narrow phenological windows by the rapid maturation of foliage. Summer feeders, are somewhat buffered from the effects of cooler temperatures because they are able to feed on nutritionally poorer food and thus have a longer phenological window in which to complete development. Again, my point is that the pooling of Lepidoptera into a single biomass variable will likely obscure some of the critical aspects of temperature that may be present in the data. Such analysis might elevate the importance of the conclusions drawn in this paper.

(3) Overwintering temperature. I think that few would be surprised by the finding that there was no significant relationship between low temperature and seasonal abundance of caterpillars. I would submit that the relationship between Lepidoptera and

overwintering temperatures is much more complicated than this crude measurement can encompass. While temperature minimums certainly can be lethal, most native insects in the region are going to tolerate all but the most extreme minimums with little problem. A more interesting question might be the time of year when the temperature extremes occur. If the minimum extreme occurs in mid March rather than mid-January, the effect might be considerably more important given that diapause may have been broken and cold tolerance diminished. What about years with big swings between warm and cold (like 2005-2006), or years with extended periods of very warm or very cold winter temperatures? The author's do offer one qualifier, snow depth, which has been documented as being important for some species, such as gypsy moth (see Andresen et al. 2001), but I think discussion of the weaknesses in this very general treatment of winter temperature are warranted.

(4) Time lags. There was no examination of the potential for time lags in the analysis of tree growth or winter temperatures on insect populations. While this might be appropriate for winter temperatures (but not necessarily), the response of slow growing trees and their chemical composition may occur on a longer time scale.

(5) Ring growth and tree chemistry. I do not believe that the analysis of ring growth is a particularly good surrogate for tree chemistry. Many studies have shown a high degree of within and between season variance in tree phytochemistry. I submit that using tree ring data to make inferences about primary and secondary leaf chemistry is a stretch. I'd like to see some data or some citations that indicate that this is a valid approach in natural systems. Most of the reference used to support this approach are for studies in highly manipulated, artificial settings, or are review / synthesis papers. None, to my knowledge have empirical data supporting the tree chemistry – growth rate supposition advanced by the authors.

(6) The last sentence of the abstract, to me, implies that this study shows that change in caterpillar density influences herbivory levels and the abundance of natural enemies. While this is likely, this study did not examine this question. Rather, it showed only that there was a correlation between caterpillar density and summer thermal accumulation. This should probably be reworded to reflect more accurately what was actually done.

(7) Hypothesis 2 is phrased as “ long, warm summers.....”. In fact, the authors did not test for changes in summer length but only for thermal accumulation. Thermal accumulation could be the same in a short, hot summer or a long, cool summer. This measure can not separate the two.

(8) Figure Caption 1 seems to have the author(s) notes or comments inserted into the text.

(9) perhaps a semantics issue, shouldn't the title read Northern Hardwood Forest, not Hardwoods?

Subject: Decision for MS# 06-0512

Dear Dr. Ayres,

Thank you very much for submitting your manuscript "Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis* (Coleoptera: Scolytinae)" (Article) for review by Ecological Applications. The reviewers and I appreciate the work you have accomplished. Based on the reviews, we are willing to consider a revised version for publication in the journal, assuming that you are able to modify the manuscript according to the recommendations.

Your revisions should address the specific points made by each reviewer. I would like to draw your attention especially to the specific and constructive suggestions by the second reviewer: you must include more information about the measurement set-up and analytical procedures; the sections headed "Application to management" and "General utility of relating climate, physiology, and population dynamics" should be combined and re-written in the flavor of proper conclusions to the paper.

You should also send a cover letter, indicating your response to the review comments and the changes you have made in the manuscript. If you disagree with a reviewer's point, please explain why.

Sincerely,  
Subject editor

-----  
Reviewer #1 (Comments to Author):

This is a very well written paper that describes an equally well organized and executed set of research activities. My objections are niggling, in that I found:

- the two Y captions confusing in figure 7 (how can the probability of mortality be greater than 1?),
- the relative changes in temperature a bit obtuse on page 17, line 22,
- the description of the thermal buffering model on page 19, lines 13-16 a bit confusing, and
- the description and discussion of the theoretical model of *D. frontalis* population dynamics to temperature on pages 15-16 and page 23 somewhat incomplete. Perhaps it is due to my unfamiliarity with Ungerer et al., 1999, but I read that article, and only after a fair effort was able to puzzle out their methods and significance, I think. The authors may want to review their treatment of this aspect of their work, and modify it if they feel they can make it clearer.
- minimum is mis-spelled on page 31, line 14.

On the whole, this paper was a joy to read, quite good at mixing biological observations, a theoretical understanding, and models to add knowledge of specific life history characteristics and population dynamics. Well done.

Reviewer #2 (Comments to Author):

Abstract

The authors need to expand the abstract to include essential details on the timing and location of the study: when it was done and what time period do the data apply to? Other than saying they used 1439 pairs of site-years, the authors are silent with respect to details of "when and where" with respect to the work

## Introduction

In the Introduction the authors suggest temperature as the best exogenous driver of insect populations essentially because it is known to affect insect physiology and insect survival, and because temperature is a very widely measured climatic variable. Thus, their contention to use temperature to build a model of population dynamics is reasonable. However, they provide no clear rationale for why winter temperature is the key temperature variable. We must infer that if the temperature is low enough, a lot of insect larvae will be killed and thus diminish the next year's population. This is reasonable, but it seems to me that given the sophistication of the rest of the paper some more convincing front-end argument is needed to set up the work.

The essential details are supplied as part of the section titled Study System, but it would help to include some details of the reasons in the Introduction.

## Study System

Page 6, lines 14-17. The specificity of the claim of the temperature on one winter night in a whole year dropping to  $-16^{\circ}\text{C}$  somehow defining or "being in concordance" with the northern limit of the southern pine beetle seems too strong a statement to me. I have never heard of such a fine temperature requirement defining an effective spatial limit. I assume it is air temperature that is being referred to. Also, I suggest further explanation of exactly what is meant by the statement "allowing for  $1^{\circ}\text{C}$  buffering of temperatures in the phloem.." Does this mean that the minimum can go to  $-17^{\circ}\text{C}$ ?

Page 7, line 1. Authors need to explain their statement that the data from 50 weather stations in the model "ignored the effects of elevation and microclimate.." Are they suggesting a problem of not adjusting temperature data from the height of measurement in the screen (1.5 m) to some other height, or are they referring to an actual topographic effect on temperature patterns. A similar comment is applicable to their use of the term 'microclimate'.

## Methods

Page 8, lines 14-18. Change of point size.

Page 8, line 21. Authors need to define their use of the term 'lapse rate'. Is it to be taken literally to mean actual or environmental lapse rate or is it a surrogate for a height-dependent weighting coefficient in their interpolation model (equation 1)?

## Phloem temperatures

Page 10, starting at line 15. I found the description of the experimental work very brief and quite inadequate for a reader to understand how the authors solved for K, the rate coefficient in the thermal model of the behaviour of tree temperature (their Newton's Law of Cooling). Nine trees were instrumented at five places. There is no mention of depth of measurement of the thermocouples, no mention of age of tree, no mention of height of measurement in the tree, and no discussion of possible effects of other variables such as wind speed that would affect, to some degree, the value of heat loss from the bole.

Page 18, line 23. The relation of K to dbh is very weak indeed.

## Physiological measurements of cold tolerance

Page 11, line 21. Authors need to augment the description of the experiments conducted to determine the lethal temperatures. Like my last point, the experimental description of cold tolerance determination leaves out important details. How were the thermocouples attached to the insects? What determined the two cooling rates? By implication, rate does not matter, but reaching crystallization does.

Page 12, lines 9 to 17. I find this paragraph quite confusing. In line 9, with respect to the comment on lower lethal temperature, the question is "lower compared to what?".

Page 12, line 20. Why  $-15.3^{\circ}\text{C}$  and not  $-15.6^{\circ}\text{C}$ , one of the supercooling points (see same page line 11).

Either on page 19 or in the caption to Figure 4, authors must tell the reader where the 25 sites are located. Now they only say in the southeastern US, with one outlier in WV. I would suggest some more specific locations would help the interpretation.

#### Application to management

I did not find that this section added much to the content of the paper. It could easily be deleted or some minor points on the relevance of the findings to management (all minor) could be added to the Conclusions.

#### General utility of relating climate, physiology, and population dynamics

I found this section unhelpful. It strays into a very general discussion of modelling population dynamics and seems to bear only very marginal relevance to the content of the work reported in the paper. The basic point made is that the model developed for southern pine beetle is general enough to be applied to other species. I believe that such a claim needs further justification that has not been argued convincingly by the authors.

The paper would profit from a Conclusion.

From: oecologia@zoology.ufl.edu  
Date: Tue, 3 Jan 2006 17:06:28 -0500 (EST)  
Subject: Oecologia - OEC-CWO-2005-0938

03-Jan-2006

Re: Fitness consequences of pheromone production and host selection strategies in a tree-killing bark beetle (Coleoptera: Scolytidae)  
Decision: Revision

Dear Dr. Pureswaran,

Your manuscript has been reviewed for Oecologia and one of our editors (name deleted by MPA) has made a recommendation of "Revision". I concur with that recommendation (as you will see the reviews were quite positive). Please see the comments of the Editor and Reviewers below. Please address the points raised in the reviews in a revision of your manuscript and then submit your revised manuscript at <http://mc.manuscriptcentral.com/oecologia> within 60 days.

In your cover letter, please indicate how you have responded to the individual reviewer's comments. Of course, if you disagree with specific comments raised in the reviews, feel free to respond accordingly in your letter. The subject editor will be notified when you submit a revision and will continue to handle the review of your manuscript.

Thank you for considering Oecologia as an outlet for your research results. I look forward to receiving your revised manuscript.

Sincerely,  
Editor-in-Chief, Oecologia

\_\_\_\_\_ comments \_\_\_\_\_

Handling Editor comments:

Handling Editor: 1  
Comments to the Author:

Dear Dr. Pureswaran,

I now have two reviews of your manuscript, one from ... and the other that I wrote. We both felt that this manuscript will make a strong contribution to the field and that it addresses issues that have not received a lot of prior work. Ref 1 had numerous suggestions, although they can all be made relatively easily. They should help clarify what you did and the interpretation of your results that the reader gets. I had very few suggestions for improving this manuscript. I hope that you will incorporate these suggestions into a revision. Please don't hesitate to call me (or ref 1) if you have any questions.

Sincerely, .....

Reviewers' comments to author:

Reviewer: 1

Comments to the Author

This article addresses an important question, that is of general interest to readers of *Oecologia*. It is very well written. The Tables and Figures are crisp. The experimental approach is appropriate, and moreover, shows a willingness to tackle a very difficult subject, individual variation. One limitation is that only one tree at each attack stage was studied. However, this work requires such careful and repeated analyses through time, that in my opinion if large sample size at the whole-tree level were held as a requirement, these interesting patterns would never have been detected. I think observations of individuals, such as reported here, are valuable.

Chemical analysis methods, and Statistical analyses, are appropriate.

There are some instances where Methods should be reported more clearly, terminology adjusted, or conclusions tempered. These are listed below. They can all be addressed by wording changes, and hence I consider this a minor revision. Some of these suggestions are simply that, and I've indicated they should be left to the authors' prerogative.

Significant points (but easily addressed):

1. Line 138: From the description, these appear to be naturally occurring rather than pheromone - induced attacks. This should be stated explicitly. If pheromone-induced, then that substantially impacts interpretation.
2. The term "scrounger" denotes a separate type of behavior, which is not documented here. It also implies a conclusion. Replace with neutral terms that have no such connotation and are already in the literature, such as "early vs. late arrivers" or at most, "pioneers vs. joiners."
3. The results support your conclusion that there is no phenotypic plasticity in pre-landing pheromone capability between early vs. late arrivers. But the statements in the Abstract (line 38) and Discussion (line 280) are subject to misinterpretation as written (i.e., no phenotypic plasticity relative to prior colonization). The host provides an element of phenotypic plasticity - Landing and boring beetles produce different profiles, host-converted pheromones far exceed de novo pheromones, and host precursors change through time. This can be clarified by inserting "pre-landing pheromone capability" in each of these sentences.
4. Because you found host-converted pheromones far exceed de novo pheromones, and it's known that inter-tree variation is high, qualify your interpretation a bit with the fact you studied only 2 trees. Larger sample size at the tree level could yield different results, and at least allow for a test of the tree component, so perhaps state something to that effect.



5. Line 227: "Differences between sexes largely eliminated post landing": Fig. 2 is cited here, but Fig. 2 shows beetle performance not pheromone data. More importantly, Table 1 which shows pheromone data does not appear to support this statement.
6. Similar to #3 above, the sentence on line 286 is correct in the context you state it, but vulnerable to misinterpretation once cited several times (trust me - advice from a veteran who's been there): Your data support the possibility of alternate phenotypes between virgin and re-emerged landers as per Coster, but as you state elsewhere not alternate phenotypes between virgin early- vs. late-landers. Embed the latter in this crucial sentence.
7. The experimental design only allows for performance data on the subset of landing insects that successfully made it into the tree. Thus, comparisons between early and later arrivals assume this proportion to be equal between these groups. That seems unlikely. Predators that feed on arriving adults are attracted to the pheromones of the first beetles that enter, and so likely have a disproportionate effect on later arrivals (Aukema & Raffa 2004). I don't think this changes your fundamental conclusion, but it enters into the overall equation.

Minor points:

1. Line 113: I appreciate the citation, but actually Birgersson et al. 1988 developed this idea before us, so their name should be inserted ahead of ours. Also, change "should" to "might".
2. I can anticipate a reviewer arguing this is pseudo-replicated because there is only 1 tree of each category and aggregation occurs at the tree level. However, if that criticism arises I would dispute it. This paper is written from the individual beetle perspective, and so beetle is the experimental unit (with some qualifiers as per #4 above).
3. Because the pheromone profiles of males and females are so different (Table 1 shows there are essentially male pheromones and female pheromones), might it be cleaner to perform separate statistical analyses for males and females (lines 184-192)? Of course that would drop the \*sex interactions. I think Fig. 1 would be easier to read if males and females were separated. These suggestions should be left to the authors' prerogative, as either way is appropriate.
4. Lines 232-245: This is incredibly interesting information!!
5. Lines 251-264 and fig. 2. I suggest showing the gallery length data rather than describing it as 'data not shown'. It goes straight to your question. If anything, I think offspring per capita per day can be omitted from the figure and simply described in text. Or include both. I think best of all would be to show gallery length per capita and gallery length per capita per day (and omit offspring per capita per day because it is related to gallery length per capita per day), because the latter really goes to the heart of your argument under "Timing of attack and beetle fitness" (line 327-325).
6. Lines 273-278: These sentences don't seem to fit anymore, given your results. I suggest deleting and moving straight to your main point, on line 279.
7. Line 279: As per #3 above, specify that this refers to pre-landing pheromone production capability.
8. Line 336: "As predicted ...". Isn't this actually counter to your prediction (line 73, and Intro)? Rerword?
9. Perhaps divide Table 3 into a,b,c, and d to make it easier to distinguish different sections. ... Authors' prerogative.

10. Lines 326-7, 330-1, 334-5: Yes, your data make a good case for this. Relative gallery excavation per day among stages of entry are also in Raffa & Berryman 1983 p31 lower left.

11. I suggest changing "indicate" (line 346) to "are consistent with the view" and inserting "some of" after "avoid" on line 348 to qualify things are bit.

12. Line 412: Italicize "Dendroctonus".

I think this represents a fine piece of work.

I do not wish to remain anonymous. If any of my comments are unclear, the authors are welcome to contact me and I will try to give a more adequate explanation. But there is no need to do so.

Name of reviewer was given here

=====

Reviewer: 2

Comments to the Author

This manuscript was a delight to read. The question was very well motivated by the introduction. The results were presented very clearly and I was truly interested in knowing what you found out. The paper was particularly well written.

I agree that selection may be stabilizing for arriving at the middle of the mass attack. However, I was not fully convinced that a tradeoff wasn't also occurring. Early arrivals produce smaller galleries and have reduced fitness. Do the small galleries explain all of the variance in fitness that can be explained? What happens if you examine the effects of arrival time on fitness with gallery size as a covariate?

I am not familiar with REGW multiple comparisons. Perhaps include a sentence explaining why they are particularly appropriate.

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You may also log on to the Author Center at <http://mc.manuscriptcentral.com/oecologia> to see this letter and any attachments (click on "view decision letter").

Dear Dr. Ylioja,

Manuscript 2004-FS-091, "Mismatch between herbivore behavior and demographics explains scale-dependence of host susceptibility in two pine species" has been read by an Associate Editor and 2 outside reviewers. The AE and the reviewers liked the manuscript, but each had some minor editorial comments which you need to attend to. Their comments are included below. I think your manuscript will be acceptable for publication in Forest Science following the changes recommended by the reviewers.

When you revise your manuscript, please consider each of the review comments, and indicate your responses to them in a rebuttal letter submitted with the revised manuscript. You may choose not to make all suggested changes in the manuscript; however, you must indicate what your response was to each of the major suggestions.

A revised manuscript must be submitted within one year of the date of this message. If a revision is submitted after more than one year, it will be treated as a new submission.

When you prepare the revision, please carefully read and follow the Forest Science style requirements at: <http://www.safnet.org/periodicals/forscience/forsciguide.cfm>.

These include listing specific page numbers you reference in any books or monographs, formatting any tables in portrait orientation, and making sure your tables do not have vertical lines in them. Be sure that all text citations correspond with the Literature Cited. Also, for citations, the second and following lines should not be indented. Make sure the entire manuscript is double-spaced. Also, remove numbering of headings and subheadings. Upon completing your revision, please submit it online

Author instructions may be viewed at: [http://forsci.allentrack.net/cgi-bin/main.plex?form\\_type=display\\_auth\\_instructions](http://forsci.allentrack.net/cgi-bin/main.plex?form_type=display_auth_instructions).

Finally, follow this link to submit your revised manuscript: <http://forsci.allentrack.net/cgi-bin/main.plex?el=A5BU4FZ3A1IM1I3A9QEZKVEO4fLYquqcamWOOgZ>

I appreciate your effort and I look forward to publishing your paper in Forest Science.

Best regards,

Editor  
Forest Science

%%  
%%

Associate Editor(Comments):

lines 12 - 15 , p. 6 should be removed.

Associate Editor(Comments to Author):

The editor could not find Ungerer et al. 1999 in the text. If it is there, great, if not please remove from the Literature Cited list

Thank you for your well written and thoughtful submission. I am pleased to say that both reviewers considered this manuscript suitable for publication with minor revisions. Please use the recommendations of the reviewers to help with your revision. If you disagree with any recommendation, it is your right to say so, but I agree with their comments and hope you will to.

The review process took longer than I had hoped. I prefer 3 reviews, but after receiving the two reviews, I felt we had to move forward.

What follows are some recommendations from me:

p. 1, L5 - I recommend replacing "host organization" with "geographic scale." The former sounds like a group that meets every so often.

p.3 L5-8 - No mention is made of relative host susceptibilities to SPB. Would it be helpful to include such information?

p5. My take on Va pine being a less suitable host has to do with the fact that the resin does not crystallize very fast and beetle brood have difficulty developing under those conditions. Although I can't cite a paper offhand, it would seem to me that this has been documented before. Can you comment on this when you submit your revision?

Lit cited section: Include # of pages for books, not just pages from the chapter.

Figs, upper and lower is not typically used. Can you change to fig 2a,b, 3a,b, and 4a,b?

%%%%%%%%%%  
%%%%%%%%%%

Reviewer #1(Comments to Author):

December 10, 2004

This manuscript is a logical follow-up to Veysey et al, which evaluated host preference differences in southern pine beetle. The current manuscript extends the prior results to landscape - level interpretations. This is a good manuscript - on point, well written, and interesting. I have a few suggestions, which are listed below. Most are of a rather minor nature, and I believe they can be addressed rather easily. I do not wish to remain anonymous.

Reviewers name given here.

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1. Title: I suggest changing "explains" to "contributes to". That leaves the door open for future research.
2. Pg 2, l 3: I'm ok with calling bark beetles "Scolytidae", but some get quite upset by it. Whichever you prefer;
3. Pg 2, l 23: scales - plural
4. Pg 2 l 14: I think "absolute" is a more appropriate word than "intrinsic";
5. Pg 3 line 16: This wording makes it sound like beetles aggregate at places other than on trees - reword.
6. Bottom of pg. 4 - Top of Pg. 5: This paper hinges on beetle reproductive rates being lower in Virginia pine than loblolly pine. So that needs to be presented unambiguously to convince your audience. Normalize for beetle attack density and tree size, which affect progeny per attack. This will help the reader understand if it's likely due to resistance, small size, etc. I'd delete "may also be related to oleoresin chemistry" if you don't know.
7. Pg 6 l 8: spelling of Liquidambar;
8. l 13-15; this doesn't fit in Methods section
9. Figure 4: Restrict age axis to age ranges of trees that southern pine beetle commonly attacks. The youngest trees in the data set are 37 yrs (Table 1). The power of simulation is that you can extrapolate beyond that, so you needn't restrict it to 37+yrs. But even so, make it more biologically realistic by truncating this axis to a reasonable age @20 yrs?

10. Sometimes in the Discussion and Abstract it was not always apparent what was based on simulations vs. actual data, or more precisely when simulations extended beyond the value limits of the available data. That should be clarified.

Following a minor revision this should be suitable for publication in Forest Science. I hope these comments are helpful.

%%%

Reviewer #3(Comments to Author):

Most of the information presented is not new. These characteristics of SPB are generally well known, at least to researchers. However, this paper nicely quantifies the information which has been previously done on piecemeal basis or not at all.

The data cited from a previous paper on brood production (Veysey et al. 2003) may be a bit misleading. Brood production from Virginia pine is not as low as it appears relative to loblolly if it is shown as production per square meter because the low "per attack" production is offset by higher attack densities on Virginia pine.

There are a couple of minor editorial items:  
P. 12, L 16 - Insert "of" between mortality & Virginia  
Abstract, L 8 - "flying beetles" do not attack. They land first.  
P 6, L 14-15 - irrelevant

Ref.: Ms. No. FORECO1167

Effects of fire and mechanical wounding on *Pinus resinosa* resin defenses, beetle attacks, and pathogens  
Forest Ecology and Management

Dear Dr. Lombardero,

I can now inform you that the Editorial Board has evaluated the manuscript FORECO1167: Effects of fire and mechanical wounding on *Pinus resinosa* resin defenses, beetle attacks, and pathogens.

The Editor has advised that the manuscript will be reconsidered for publication after revision.

The comments below should be taken into account when revising the manuscript. Along with your revised manuscript, you will need to supply a covering letter in which you list all the changes you have made to the manuscript, and in which you detail your responses to all the comments passed by the reviewer(s) and the Editor. In addition, please highlight the changes in the revised manuscript. Should you disagree with any comment(s), please explain why in your covering letter.

To submit a revision, please visit <http://ees.elsevier.com/foreco/> and log in as an Author. You will see a menu item called Submission Needing Revision. The revised manuscript and covering letter can be submitted there.

Kind regards,

Editorial Office Forest Ecology and Management

Reviewers' comments:

Reviewer #1: This paper is very well written overall, and I believe it can be accepted with some revision, as described below. The subject of this study is the effects of biotic and abiotic stresses on the resin flow of red pine and consequent resistance/susceptibility to bark beetle attack. I believe this is an important study that should be published since resin is considered one of the main defensive tools used by conifers against physical traumas and biotic attacks.

In conclusion, I recommend publication of this paper in Forest Ecology and Management, provided my specific comments/suggestions below are dealt with.

page/line number

3/2

Oleoresin may be the primary defense against insects, but certainly not against pathogens. Just think pitch canker or diplodia blight, in which the pathogens grow happily in resin soaked tissues. This statement needs to be modified accordingly. Even the reference appears to refer only to insects.

3/24

Replace "□resin is□" with "□resin are□".

Materials and methods

This is a rather complex design and I think the paper would benefit greatly from a diagram of the treatments on the individual trees, with relative positions of wounds, inoculations, resin taps, fire scars, etc. All this is very difficult to describe verbally and I had quite a bit of trouble picturing all these items in my head and I suspect other readers might also have some trouble understanding the design.

6/10-13

How were all these temperatures, energies, etc. measured? I am particularly intrigued by the measurements of the cambium temperature.

6/21

Replace "□trees□" with "□tree□".

7/1-9

I found this paragraph particularly confusing. As I understand it (the diagram suggested above would be very useful, I think) the wounding strips were first 4 cm high and then 6 cm high (after removal of another 2 cm). Lines 1-5 are particularly confusing in this respect, because one tries to follow a logical, chronological thread, but the authors begin with the final wound height, so I was perplexed for a while as to the relative positioning and height of the various wounds. Also, where were the resin taps positioned relative to all these wounds, and the various resin taps at various dates? Wouldn't proximity of the various resin taps to each other and to the wounds give suspicious resin flow readings?

7/11

This subheading sounds like the trees were being attracted to the beetles. I suggest "Attraction of bark beetles to burned and wounded trees"

7/12-22

The authors need to provide more detail as to how the 42 trees were assigned to each treatment. Also, how would the band of food wrap be positioned relative to the wounds? Wouldn't the resin from the wounds alter the catches? Most importantly, the rationale for using pheromones needs to be explained: Wouldn't the pheromones trump all other attractants? Why use them in the first place? Wouldn't the result in Fig. 4 be expected in these circumstances, since all trees in that figure were baited with pheromones?

8/4-6

I am unclear about the inoculation procedure. Did the authors use a slurry of mycelium? Did they use a tiny plug of culture coming out of the hypodermic syringe needle? Were the wounds and the inoculum plugs really 3 mm and 1 mm in diameter? Those are hardly feasible, in my mind, particularly in the bark of relatively large trees. Did the lesion measurements include the perforation, whatever its diameter?

8/16

Specify which software was used for all the analyses.

9/8

Replace "□flow□" with "□flows□".

10/10

Replace "□vs□" with "□and□" in both cases.

10/12

Perhaps point out that burned trees had ~50-60% the resin flow of controls, even if this was not significant (P = 0.13 is pretty close to significant).

11/10-15

A photo would be extremely useful here.

11/18-24

Again, why would you expect any different, since the trees analyzed were baited with pheromones? Am I missing something? Given this problem, as I see it, perhaps the authors should not even bother presenting the landing data in a figure and concentrate instead on the attacks, which no doubt they were trying to induce with the pheromones. In other words, the authors should just state that the attraction with pheromones was successful and that it insured equal presence of beetles on all trees. Differentiation then occurred at the attack phase.

12/6-8

A photo would be extremely useful here.

12/21-23

Any correlation here between length and depth of lesions? It would be interesting and very useful to know.

12/23-13/1

This confirms my contention that oleoresin is not a primary defense against pathogens (see my first comment above).

#### Discussion

General comment: the authors concentrate on the constitutive resin system and completely ignore the induced resin system. How do they know the extra resin is all from the preformed system? The authors should review, for example, the work by Franceschi et al. in spruce (e.g. Nagy NE, Franceschi VR, Solheim H, Krekling T, Christiansen E (2000) Wound-induced traumatic resin duct development in stems of Norway spruce (Pinaceae): Anatomy and cytochemical traits. *American Journal of Botany* 87: 302-313), and more recently by Luchi et al. in pine (Luchi N, Ma R, Capretti P, Bonello P (2005) Systemic induction of traumatic resin ducts and resin flow in Austrian pine by wounding and inoculation with *Sphaeropsis sapinea* and *Diplodia scrobiculata*. *Planta* 221: 75-84) on the formation of traumatic resin ducts. Interestingly, Luchi et al. also found no differences in systemic induction of resin flow between wounding and inoculation with pathogens, which might reflect the results of this paper, at least in part. Invocation of a dynamic constitutive (preformed) system is OK, but not sufficient (see lines 12-17, p. 13, and lines 3-4, p. 14).

14/4-7

It seems to me that the authors are confusing the concepts of hypersensitive response, necrotic lesions, and resin response. Formation of lesions in response to pathogens, formation of polyphenolic parenchyma cells, traumatic resin ducts, accumulation of phenolics, lignins and resins, etc. are all inducible responses. Some of these may be more important with pathogens, for example accumulation of phenolics and lignins. That resin flow is not correlated to lesion size in this paper is not quite surprising to me (see my first comment above). These points should be expanded a little.

15/4

Replace "attractiveness" with "palatability"? (There were no differences in attractiveness as measured by landing rates.)

15/8-9

Again, perhaps I am missing something, but how can the authors make this statement when the beetles were attracted to the trees with pheromones (Fig. 4)?

15/17

Replace "are attracted to" with "preferentially attack"?

16/3-6

It seems to me the authors are over-reaching in their co-evolutionary interpretations: (1) they do not know the exact timing of the attacks, which might have occurred during the high-resin phase; and (2) the lag in resin flow increase may just be incidental, a function of tree physiology (perhaps the time consuming need to form traumatic resin ducts?), rather than an evolutionary adaptation to this particular insect group.

16/9

Why "facultatively" if, as the authors claim, this is an evolutionary adaptation to fire? In other words, this is not a facultative event if trees will always respond to low level fire with eventually increased resin flow.

#### Figure legends

1) The figures are all necessary, unless the authors decide to eliminate the analysis of the landing rate data (as I suggest above), in which case Fig. 4 is not necessary.



- 2) More detail needs to be given in the figure legends. They should all be essentially self contained descriptions of the various charts.
- 3) Lettering should be used to identify significantly different treatments, where appropriate, to ease interpretation of the graphs.
- 4) A different color scheme in the charts would be helpful, e.g. black, white, and grey bars instead of hatched bars (especially fig. 3).
- 5) Shouldn't the raw data be used in Figs. 4 and 5, instead of the logs? In fig. 5 it's not readily apparent that attacks in burned trees were more than twice as high as in unburned trees (p. 12, l. 1), because logs were used.
- 6) In fig. 6, "procera" should be "procerum"?

Reviewer #2: Reviewer #2 - Comments on Lombardero et al. - "Effects of fire"

This is a very well written manuscript describing an elegant, fairly comprehensive experiment which should be a valuable contribution to the literature on tree-insect-fungus interactions. The authors are particularly to be commended for addressing multiple agents of disturbance simultaneously. While the authors overstep their data a bit in the discussion, with some revision and additional qualifying statements, this paper should be very well suited for publication in *Forest Ecology and Management*. Specific comments are given below.

Page Line Comment

3 17 Should be "bark beetle", not "bark beetles"

4 2 Resin flow is "assumed to be relevant". A comment as to whether this paper supports or refutes this assumption would be a good addition to the discussion.

4 11 The authors do a pretty good job of admitting this, but it is important to emphasize that the area of tree sampled for resin is key. Where did Santoro sample? Presumably from the zone of burning. Resin flow elsewhere in the tree is likely to be very different.

8 4 Not an accurate statement. Klepzig et al. 1991 did not report any *L. terebrantis*, *L. procerum*, or *O. minus* from either *Ips* species. They did recover *O. ips* from all *Ips* they sampled. Rephrase as follows: "All are native fungi that naturally infect *P. resinosa*, and are frequently associated with red pine infesting bark beetles and weevils (Klepzig et al. 1991).

Fig. 1 & 2 Label graphs with letters indicating significance.

Fig. 4 & 5 Present untransformed data in the graphs. The figure captions say nothing about transformed data, and the decimal values/ tree are hard (for me) to interpret as biologically meaningful landing densities. Very confusing as it is now presented.

Fig. 6 Legend: Should be (as it is in the text) "*Leptographium procerum*" not "*procera*".

13 20 Need to indicate (here or somewhere in the discussion) even more clearly that all the studies of this nature so far have indicated only localized induced resistance (not systemic). This includes the cited work by Klepzig, and Christiansen.

14 7 Should be "Paine" not "Pain"

14 14 Should be "lesion lengths" not "lesions length"

14 22 This is very likely only true for beetles attacking within areas that were

previously attacked (or wounded, or burned, or inoculated). Need to be clear that systemic induced resistance is not being proposed here, nor can it be inferred from previous work.

15 4 "attractiveness" is not the appropriate word in this context. To most, I suspect, it will indicate primary attraction (pre-landing, in-flight). "acceptability" would be a better word choice in that it allows for the apparently random landing followed by touching, tasting, biting, sampling, etc. to determine suitability for colonization.

15 17 Again, I don't think the data supports "attraction" per se. This is a loaded term with a volatile history, and the tests the authors conducted to actually evaluate this did not demonstrate primary attraction. Fig. 4, if anything, seems to indicate slightly lower landing rates on burned trees.

16 3 Not a very successful adaptation for Ips, apparently. None of the attacks succeeded. This brings up a very important point. Nowhere in the paper do the authors discuss the natural history/ biology of these Ips. These are non-aggressive beetles that cannot and do not kill healthy trees (or even, apparently, burned-wounded-inoculated trees). The frequent comparisons the authors make to work on aggressive, tree-killing beetles are disingenuous or misleading. Clearly describe the biology up front and indicate that these beetles are most often only contributing factors in tree death.

16 8 Should be "prevent bark beetle attack", not "prevent bark beetles attack"  
--- end of quoted text ---