

March 11, 2016

Dr. Jatin Kala
Topical Editor
Geoscientific Model Development

RE: Submission of a revised manuscript to Geoscientific Model Development

Dear Dr. Kala,

We are pleased to submit the revised version of our manuscript titled “Implementation of a Marauding Insect Module (MIM, version 1.0) in the Integrated BIOSphere Simulator (IBIS, version 2.6b4) Dynamic Vegetation–Land Surface Model” to Geoscientific Model Development (GMD). We want to thank both Reviewers for their supportive assessment of the previous version of our manuscript, as well as for the comments they provided to help us improve it. We are confident that we have satisfactorily addressed these comments and that our revised manuscript meets the high quality standards of GMD.

You will find below our responses to the comments from the Executive Editor, Reviewer #1, and Reviewer #2 (as uploaded earlier today on the Discussion website of GMD), as well as the ‘track changes’ version of our revised manuscript. Regarding this last element, we would like to bring three minor points to your attention:

- In the Introduction (page 3, first paragraph), many references appear as deleted; actually, we simply updated one of them (there seems to be a minor issue with the LaTeX Copernicus package when tracking changes in references). For any doubt, please refer to the normal version of our revised manuscript.
- The number of studies used for the comparison presented in Table 4 went from 37 to 38, following a suggestion from Reviewer #1. We forgot to note this change in our responses 1.11 and 1.24 below.
- There is a very minor difference (a single comma) between our actual revised manuscript and the text we provided in responses 1.2 and 1.16 below (the same modified sentence appears in both responses 1.2 and 1.16).

Best regards,

Jean-Sébastien Landry
McGill University (now at Concordia University)

Interactive comment from Astrid Kerkweg (Executive editor): please note that the interactive comment is in italics, with our response given in a regular font.

Dear authors,

In my role as Executive editor of GMD, I would like to bring to your attention our Editorial version 1.1:

<http://www.geosci-model-dev.net/8/3487/2015/gmd-8-3487-2015.html>

This highlights some requirements of papers published in GMD, which is also available on the GMD website in the ‘Manuscript Types’ section:

http://www.geoscientific-model-development.net/submission/manuscript_types.html

In particular, please note that for your paper, the following requirement has not been met in the Discussions paper:

- Inclusion of Code and/or data availability sections is mandatory for all papers and should be located at the end of the article, after the conclusions, and before any appendices or acknowledgments. For more details refer to the code and data policy.*

Please move the Code Availability section to the correct place in your revised submission to GMD.

Yours,

Astrid Kerkweg

>> E.1 We thank you for helping us better meet the editorial requirements of GMD. We moved the “Code availability” section before (instead of after) the appendices. <<

Comments from Reviewer #1: please note that the review of our manuscript is in italics, with our responses given in a regular font.

GENERAL

Overall, the research done is substantial and the manuscript is well written. The manuscript can be clearly divided into two major parts: (1) a methodological part, describing the implementation of a new insect module (MIM) into an existing land surface model (IBIS); and (2) a simple application of a part of the new IBIS-MIM, illustrating the simulation of a stand-replacing bark beetle disturbance and its impacts on ecosystem cycles at three locations in western Canada. Implementing insect disturbances into large-scale ecosystem models, such as IBIS, is challenging when going beyond a single species or region. The concept of insect functional types (IFTs) is applied for the first time in this study, allowing the assessment of different insect disturbances at different regions within a single framework. This step means a significant contribution towards an appropriate representation of insect disturbances in ecosystem models in general. Moreover, the study provides incentives for coupling MIM with other models than IBIS, and for the future implementation of additional IFTs. The only aspect a reader will probably miss is a more comprehensive application of the implemented features. For instance, defoliator-induced damage, different levels of bark beetle-induced mortality and large-scale, quantitative effects on ecosystems (all of which can potentially be done with IBIS-MIM) have not been simulated in the context of this study.

>> 1.1 We thank you for this positive assessment of our manuscript, as well as for the suggestions you provided below on how to improve it. Please note that we plan to submit other manuscripts based on a “*more comprehensive application of the implemented features*”, as the current study was indeed focussed on presenting IBIS-MIM and a simple application of this new model. This decision was based on the realization that it was too much for one paper to cover all the material in sufficient depth. <<

SPECIFIC

In the following, some specific comments (made loosely in the order of reading) may help the authors to further improve their manuscript on certain aspects:

*(1) The authors apply the concept of IFTs but they miss to give a short introduction on it (e.g., was it applied previously, and why using such types instead of species or a generic approach?). Surely the modeling community may already know the concept from plant functional types (PFTs), however, it would be useful also for a broader audience to add a short phrase to the introduction (probably useful references: Dietze & Matthes, *Ecology Letters* 2014, 17: 1418–1426, or Cooke et al., 2007, chapter 15 in: *Plant Disturbance Ecology*, eds.: Johnson & Miyanishi, p. 489).*

>> 1.2 We thank you for this suggestion. We added the following sentence right after mentioning insect functional types (IFTs) for the first time (p10369, 114). “The concept of IFTs allows simplification of the huge diversity of insect species by grouping species that cause similar impacts (Cooke et al., 2007; Arneeth and Niinemets, 2010), and has recently been applied under the name of “Pathogen and Insect Pathways” in a simple ecophysiological model (Dietze and Matthes, 2014).” We also added this last reference to another sentence (p10387, 127; modifications in italics and strikethrough): “The parameterization of IFTs was based on key outbreaking insects affecting North American forests, but could be modified to represent other insect species, *effects on other vegetation types (e.g., agricultural*

fields) and ~~probably~~, with ~~additional~~ further adjustments, effects of some vegetation pathogens (e.g., Dietze and Matthes, 2014).” Note that we also addressed another comment in the previous sentence (please see our response 1.16). <<

(2) *Is there a reason why you didn't use the most current version of soil data (version 3.2 instead of 2.1/2.2 (page 10371, line 24)?*

>> 1.3 Based on our understanding, modifications since version 2.2 were for agricultural soils: “The latest complete coverage of Canada (i.e. including areas outside the agricultural regions of the country) is v2.2.” (<http://sis.agr.gc.ca/cansis/nsdb/slc/v3.2/index.html>). <<

(3) *The required input for defoliation IFTs need to be clarified, as it is not obvious from reading. What does e.g. “5% defoliation” mean: 5% trees from a grid with 100% defoliation each, or 100% trees with 5% defoliation each? Please indicate whether or not MIM can simulate partial defoliation.*

>> 1.4 This is an insightful question and the answer depends upon the capacity of the host DVLSM. We clarified this by adding the following text after the “5% defoliation” example (p10373, l6). “For host DVLSMs that, like IBIS, do not represent many individuals for the same PFT, a 5% defoliation event translates into 100% of the trees losing 5% of their leaf area; in other DVLSMs, this same 5% defoliation event could be assigned differently, for example by removing 100% of the leaf area from 5% of the trees.” <<

(4) *In addition to the prescribed defoliation damage MIM also requires prescribed defoliator-induced mortality as input, instead of simulating emergent mortality as a result of (repeated) defoliation. You may explain why emergent mortality was not simulated, or add a phrase on that issue to the discussion of the shortcomings of MIM.*

>> 1.5 We agree with the spirit of this comment; however, we consider that this shortcoming is a limitation of IBIS (which does not simulate mortality explicitly) rather than of MIM per se. We therefore added the following sentence (p10373, l11): “In fact, for DVLSMs that, unlike IBIS, simulate PFT mortality explicitly (e.g., as a function of carbohydrate reserves), MIM would not need input data on prescribed mortality in the case of defoliators”. <<

(5) *Defoliator-induced mortality typically doesn't occur after reflush, i.e., a tree dies as a result of losing ability to reflush due to a lack of carbon resources (e.g., Cooke et al., 2007 see above). MIM doesn't consider any interaction between (repeated) defoliation and mortality, and thus in MIM a tree can reflush and die in the same season (which is not realistic).*

>> 1.6 We thank you for pointing this out. We added the following text at the end of the paragraph on reflush (p10376, l9), which also addresses another comment below (please see our response 1.9): “The value of $total_{reflush}$ for the year can be set to zero to prevent unrealistic reflush when the defoliation level is very low, or when trees have already been weakened by previous defoliation events, or if mortality is also prescribed for the same year.” <<

(6) *MIM uses fixed parameters for IFTs, e.g. start_IFT (Table 1). Since your IFT #3 (MPB) cover a large geographical range from northern BC to south-western US, how would within-species variation in parameters be attributed in MIM, by using a separate IFT for the same species? This information would be particularly relevant when applying MIM to other regions than Canada.*

>> 1.7 We think that the most straightforward way to account for within-species variation would be through the use of spatially-explicit data on parameters (similar to what is being done for soil texture). We added the following sentence at the end of the section presenting MIM (p10377, l22; DST refers to dead standing trees): “Moreover, for large-scale studies, the IFT- and DST-related parameters could vary spatially to reflect within-species variation, instead of having uniform values as we have used here (e.g., needlefall for Case #5 could occur over more than three years).” The last part of the sentence addresses a comment from Reviewer #2 (please see our response 2.15). <<

(7) *While for defoliation the time of attack is equal to the time of visible damage, there is a delay of one year from MPB attack until the damage is visible (red stage). Since MIM uses prescribed mortality data, I assume this refers to visibility / detection of damage, not to the time of attack. This point should be clarified within the paragraph where you described daily mortality for bark beetles (e.g., page 10374). Furthermore, MIM uses three years as leaf-falling rate for case #5 (Table 2), but there are two years indicated in the literature (Wulder et al., Forest Ecology and Management 2006, 221: 27–41); maybe this difference is a result of the one-year lag.*

>> 1.8 We clarified that MIM’s delay parameter refers to the time of attack in text describing the fate of all DST pools (p10377, l10; new text in italics): “The transfer of carbon from DST pools (i.e., fine roots, leaves/needles, and stems, the latter including coarse roots and branches) towards IBIS litter pools starts after a delay period and then occurs at a specific rate; *note that the delay refers to the time of attack, even for Case #5.*” Fig. 2 of Wulder et al. (2006) suggests that all trees are needleless (i.e., gray stage) ~31 months after the attack; in MIM, this actually happens ~40 months after the attack (e.g., on December 31, 2004 for an attack happening in 2001, which would last from August 1st to September 19th in MIM; see our Table 1). This small difference is not an issue, given the variability in the time needed to reach the gray stage (Fig. 3 of Wulder et al., 2006) and that longer periods have been reported by other authors (e.g., Simard et al., 2011). <<

(8) *MIM defines a reflush parameter for defoliated broadleaf deciduous trees, which corresponds to 50% of the lost leaf biomass (reference for 100% defoliation in oak). In contrast to that generic assumption based on a single-species case study, the ability to an immediate reflush is a function of the portion of defoliation (% defoliated, typically no reflush occurs when the portion is <50%) and the vitality of the tree (number of repeated defoliation events). I would suggest to mention this simplification when describing the approach (p. 10376) or in the discussion.*

>> 1.9 We thank you for these suggestions to improve precision. We added the following text at the end of the paragraph on reflush (p10376, l9), which also addresses another comment below (please see our response 1.6): “The value of $\text{total}_{\text{reflush}}$ for the year can be set to zero to prevent unrealistic reflush when the defoliation level is very low, or when trees have already been weakened by previous defoliation events, or if mortality is also prescribed for the same year.” <<

(9) *The implementation of snag dynamics is well done in MIM, yet it is not discussed sufficiently in terms of how the MIM approach differs from / or is based on previous approaches. A short phrase could be added to the discussion (e.g., 10386, 6) (beside Edburg et al., Journal of Geophysical Research 2011, 116 you have already cited, also other models consider snag dynamics, such as FireBGCv2 and FVS among others).*

>> 1.10 We were not aware of snag dynamics in FireBGCv2 or FVS, and directly based the dynamics of DSTs in MIM on empirical data from Canadian forests (please see the references provided for each of the five Cases on p10376-10377). We added a reference to these two models where we mention possible improvements to MIM (p10386, 111; new text in italics): “Moreover, MIM could be *modified by simulating the fall of DSTs probabilistically (e.g., as in FireBGCv2; Keane et al., 2011)* or enhanced by: simulating the fall of DSTs as a function of environmental conditions (Lewis and Hartley, 2005) *or the size of DSTs (e.g., as in FVS; Rebain et al., 2010)*; reducing snow albedo when needles fall from DSTs (Pugh and Small, 2012); and accounting for changes in needle optical properties as they turn from green to red (Wulder et al., 2006).” <<

(10) *You haven't provided field results for GPP, Ra, Rh, and NEP (Table 4), but I presume (without doing a comprehensive review of the related literature) there are some field studies existent. In order to further complete the table, could you please check if you can fill these open fields? For instance, Moore et al., Ecology Letters 2013, 16: 731–737, or Harmon et al., Journal of Geophysical Research 2011, 116 could probably be useful as references.*

>> 1.11 As mentioned in the manuscript (p10381, 113-14), we wanted to include only studies having actual control and effect results for the comparisons presented in Table 4 (the only exception being some studies listed in the Mikkelsen et al. (2013) review, which is a highly relevant study in this context). The NPP, Rh, and NEP results for bark beetles presented in Fig. 12 of Harmon et al. (2011) do not come from empirical data, but are rather “[h]ypothetical examples of temporal patterns” (caption of their Fig. 12); hence, we decided to not include this study in Table 4. Moore et al. (2013) is the only study of which we are aware that could have been included in Table 4 and was not. The reason we initially excluded this study was that, to be quite frank, we had a hard time fully understanding how they actually derived all their results. Following your comment, we carefully re-read the study and included their GPP results (i.e., a decrease) in Table 4. However, as far as we understand, the GPP results in Fig. 1 of Moore et al. (2013) came from satellite measurements calibrated with field-level eddy covariance data (“locally calibrated satellite estimates of gross primary production (GPP)”; their Introduction), so we added this study under the “satellite” column in Table 4. We did not add to Table 4 the results of Moore et al. (2013) on total ecosystem respiration or soil efflux, because control values were not provided after the disturbance event. <<

TECHNICAL

In addition, some minor, more technical issues:

(11) *Although the authors have already changed the title according to the editors suggestion, I still think that “version 1.0” can be skipped from the title, so that it reads more fluently without too much specifications (but that might be rather a matter of the authors taste)*

>> 1.12 We have no opposition in removing “version 1.0” if the Topical editor instructs us to do so; the current title is the one he suggested when we requested guidance on how to meet the editorial policy of Geoscientific Model Development. <<

(12) replace “...damage from broadleaf defoliators, needleleaf defoliators, and bark beetles...” with “...damage from three different insect functional types: (1) defoliators on broadleaf deciduous trees, (2) defoliators on needleleaf evergreen trees, and (3) bark beetles on needleleaf evergreen trees...” (10367, 8-9) in order to better emphasize the three IFTs, and to clarify that you don’t include bark beetles on broadleaf trees

>> 1.13 We thank you for this suggestion, which we brought as is to the text. <<

(13) add to the abstract that the application focuses only on one of the implemented IFTs, and that only a simplistic setting is used, i.e. 100% mortality in three grid cells in western Canada

>> 1.14 We added these elements to the text and also addressed your next comment (p10367, 114; modifications in italics and strikethrough): “After describing IBIS-MIM, we illustrate the usefulness of the model by presenting results spanning daily to centennial timescales for vegetation dynamics and cycling of carbon, energy, and water *in a simplified setting and for bark beetles only. More precisely, we simulated 100% mortality events from following a simulated outbreak of the mountain pine beetle for three locations in western Canada*”. <<

(14) introduce MPB as a bark beetle species (e.g., 10367, 17 or 10368, 21)

>> 1.15 Please see our response 1.14. <<

(15) use the keyword “forest disturbance” somewhere in your abstract/introduction, since it is not said at all until the section 2.2 that your model is about forest

>> 1.16 We agree that the IFT currently implemented in MIM are based on forest insect species only. However, we believe that the generic design of MIM would allow for the addition of agricultural insect species in appropriate terrestrial models (like Agro-IBIS, which is very similar to IBIS). We therefore decided to avoid deterring readers interested in models of insect impacts on agricultural systems. To clarify this point, we modified the following sentence (as mentioned in our response 1.2): “The parameterization of IFTs was based on key outbreaking insects affecting North American forests, but could be modified to represent other insect species, *effects on other vegetation types (e.g., agricultural fields) and—probably, with additional/further adjustments, effects of some vegetation pathogens (e.g., Dietze and Matthes, 2014).*” <<

(16) skip “realistic” or replace it by e.g. “approximated”, since an equal distribution of damage to the entire attack period is rather approximated than realistic (as you said in 10374, 20)

>> 1.17 On p10369, 112, we replaced “realistic” with “approximated”. On p10373, 112, we deleted “realistically”. <<

(17) replace “readily implemented”, it could give the wrong impression that MIM can just be taken and used with other models without any adaption (10369, 26)

>> 1.18 Thank you for your scrutiny; we removed “readily”. <<

(18) the sentence in parenthesis on 10374, 15-16 is not clear to me, could you rephrase it, or skip it if not really needed?

>> 1.19 We decided to entirely rephrase the sentence, as it answers a question that some readers might ask themselves: “The duration of leaf onset simulated by IBIS is much shorter than duration_{IFT} for IFT #1, so there is no risk that this defoliator of deciduous trees will consume leaves faster than their simulated onset”. <<

(19) use spelling “reflush” (instead of “re-flush”) consistently

>> 1.20 We are sorry for this lack of consistency; we used “reflush” throughout the text. <<

(20) add the time period when NPP reduction occurs (~80 yr) after “was reduced...” in 10379, 26, since NPP is balanced out after a certain period

>> 1.21 We thank you for suggesting this improvement. The text now reads (modifications in italics and strikethrough): “In the southern grid cell, on the other hand, total NPP was reduced *for about 75 years and then increased marginally for a few decades, before returning to the control level* ~~except for a marginal increase ~100 years after the outbreak~~ (Fig. 2f).” <<

(21) replace “generally” with e.g. “slightly”, since the difference is obviously very small (10384, 22)

>> 1.22 We used the word “generally” to mean that this is the case most of the time, but we agree that the difference is very small. We therefore reworded to: “Although often slightly higher at the beginning of the season [...]”. <<

(22) the long list of references is not necessary to be repeated in the conclusions, most of them are mentioned before; I suggest to skip the references from here (10387, 14-17)

>> 1.23 We removed the references. <<

(23) replace “over 30” with “37” to be more precise (10388, 13)

>> 1.24 Done. <<

(24) rephrase (or skip) the sentence in 10388, 15-16, since to my understanding the good agreement shown in Table 4 doesn't actually support "the idea that DVLSMs are valuable tools...", yet it rather supports the use of MIM as valuable tool (but that is then said in the following paragraph)

>> 1.25 This is to some extent a matter of interpretation, but we consider that the results shown in Table 4 depend more upon the responses simulated by the IBIS DVLSM than upon the changes prescribed by MIM (only one of the 28 response variables shown in Table 4 was changed directly by MIM, all the other variables being estimated by IBIS based on the new state of the vegetation). The major role of the host DVLSM is also supported by the following outcome: although the change prescribed by MIM was exactly the same in all cases, the IBIS-simulated changes differed qualitatively (i.e., increase versus decrease) across the three grid cells for some variables. <<

(25) check publication year of Landry & Parrott, probably it will be 2016 and not 2015 (10397, 9 and citation in the text)

>> 1.26 Yes, we will update this reference as appropriate (we now have a DOI, but the study is still in press). <<

(26) Figure 3: line plots (similar to Fig. 2) would probably be the better choice for (a)-(c) with regards to readability; in (d) you don't compare the three grid cells, aren't there any differences? Though being a minor issue, a consistent logic among all panels (a)-(d) (i.e., comparison of grid cells, using the same plot type and colors) may improve readability.

>> 1.27 We thank you for the suggestions. For panels (a)-(c), line plots make the data more difficult to see as the different lines often cross each other (particularly for the NEP changes in the northern and central grid cells during the first decades after mortality). Panel (d) indeed differs from the other three panels, not only because it presents the results for a single grid cell, but also because it shows absolute values for the outbreak and control simulations (instead of the difference between the two). Although this breaks the logic across the four panels, we thought it was preferable to show absolute values in this case because we wanted to show that IBIS does a good job at simulating snow accumulation at the daily timescale (such results from DVLSM are not frequently reported). Showing all grid cells would then have required six lines in panel (d), making it less readable. The results in the other grid cells differ quantitatively, but show the same general behaviour: an earlier and faster simulated snowmelt in the outbreaks simulations. <<

References (Reviewer #1)

Arneth and Niinemets (2010). Trends in Plant Science 15, 118-125

Cooke et al. (2007). Chapter 15 in Plant Disturbance Ecology, 487-525

Dietze and Matthes (2014). Ecology Letters 17, 1418-1426

Harmon et al. (2011). Journal of Geophysical Research 116, G00K04

Keane et al. (2011). The FireBGCv2 Landscape Fire Succession Model: A Research Simulation Platform for Exploring Fire and Vegetation Dynamics. USDA General Technical Report RMRS-GTR-255

Mikkelsen et al. (2013). Biogeochemistry 115, 1-21

Moore et al. (2013). Ecology Letters 16, 731-737

Rebain et al. (2010). The Fire and Fuels Extension to the Forest Vegetation Simulator: Updated Model Documentation. USDA Internal Report, Fort Collins, CO (revised: June 2015)

Simard et al. (2011). Ecological Monographs 81, 3-24

Wulder et al. (2006). Forest Ecology and Management 221, 27-41

Comments from Reviewer #2: please note that the review of our manuscript is in italics, with our responses given in a regular font.

GENERAL

Overall, the research is important and novel, and the manuscript is well written. The goal of the manuscript is to design and test an insect module that could be incorporated into Dynamic Vegetation Land Surface Models. This insect module, MIM, is designed to simulate the direct effects of defoliating insects and bark beetles (i.e. reduced biomass, mortality, and transfers of leaf litter), allowing the host DVLSM to calculate the indirect effects (i.e. reduced canopy conductance, changes in NPP, etc.). These procedures are an improvement from simply prescribing the indirect effects of insect activity without first considering vegetation dynamics. The model also simulates the lag in effective tree death from insect activity (i.e. no photosynthesis or transpiration) and actual tree fall, which is a significant improvement in modeling the various forms of tree death. The study implements three major insect functional types (IFTs): broadleaf and needleleaf defoliators, and bark beetles, and their effects on broadleaved deciduous and needleleaf evergreen trees. This use of insect functional types is novel and will open up the possibility for the effects of insect activity to be modeled regionally and globally without extensive calibration. However, MIM requires user-defined input of percent defoliation (in the case of IFTs #1 and #2) and percent mortality (all IFTs) for each year of each grid cell, rather than calculating the probability for defoliation or mortality based on the vegetation, climate, or site characteristics. This lack of a process-based method for simulating insect activity is discussed briefly in the Discussion section, but could use some more justification in the Introduction/Methods. The authors present a case study using MIM and the Integrated Biosphere Simulator (IBIS) as the host DVLSM in three grid cells in British Columbia, Canada of a control and a 100% mortality event from a mountain pine beetle outbreak (bark beetle, IFT #3). They compare changes in NPP, NEP, litter, albedo, and snow amount between outbreak and non-outbreak conditions. They also compare IBIS-MIM results to field, satellite, and model studies on the effects of mountain pine beetle outbreaks. They found that in most cases, IBIS-MIM compared favorably to what was found in previous studies. It is possible that this work could have been improved with another case study using a defoliator insect (i.e. IFT #1 or #2), as the simulation of these IFTs is different from IFT #3.

>> 2.1 We thank you for your positive review and the comments you provided to help us improve the manuscript. Regarding the “*lack of process-based method for simulating insect activity*”, we added the following two elements to the text. First, we added the following sentence (p10369, l25): “Prescribing insect activity is less sophisticated than its prognostic simulation, but nevertheless allows relevant questions to be addressed concerning the climatic and ecological impacts of insect-caused plant damage”. Second, we added the following sentence (p10373, l11), which also addresses a comment from Reviewer #1 (please see our response 1.5): “In fact, for DVLSMs that, unlike IBIS, simulate PFT mortality explicitly (e.g., as a function of carbohydrate reserves), MIM would not need input data on prescribed mortality in the case of defoliators” (where PFT stands for plant functional type). We decided to avoid adding simulation results for IFT #1 and #2 to limit the length of the manuscript, choosing instead to provide an in-depth analysis of results for the mountain pine beetle (IFT #3), for which many empirical results exist on a suite of impacts. <<

SPECIFIC

Some more specific comments that may improve the manuscript:

(1) On page 10368, line 13 the authors state that DVLSMs contain “all required” land-atmosphere exchanges, in contrast to DGVMs. What exchanges does IBIS include that other DGVMs do not? Please explain this a bit further.

>> 2.2 We thank you for raising this point. The term “DGVM” is now being used for a wide range of models in terms of the processes included and output generated. Among others, what is often missing (from a climatic point of view) in models labelled as “DGVM” are the land-to-atmosphere fluxes of shortwave and longwave radiation. We modified the sentence starting on p10368, 110 as follows (modifications in italics): “Since the term “DGVM” is often used for interactive vegetation models that estimate only some of the exchanges of carbon, energy, water, and momentum with the atmosphere (Prentice et al., 2007; Quillet et al., 2010), we will refer here to the subset of DGVMs that compute all required land–atmosphere exchanges while accounting for dynamic vegetation as Dynamic Vegetation–Land Surface Models (DVLSMs) to prevent possible confusion (*e.g., many DGVMs do not compute the land-to-atmosphere fluxes of shortwave and longwave radiation*).” <<

(2) On page 10368, line 21, introduce the mountain pine beetle as a bark beetle.

>> 2.3 We thank you for this suggestion. In response to a similar suggestion and another comment from Reviewer #1 (please see our responses 1.14 and 1.15), we modified the Abstract as follows (p10367, 114; modifications in italics and strikethrough): “After describing IBIS-MIM, we illustrate the usefulness of the model by presenting results spanning daily to centennial timescales for vegetation dynamics and cycling of carbon, energy, and water *in a simplified setting and for bark beetles only. More precisely, we simulated 100% mortality events from following a simulated outbreak of the mountain pine beetle for three locations in western Canada*”. <<

(3) At the top of page 10369, you explain how other studies on insect activity were lacking in various ways. I would suggest citing the studies that conducted each of the pitfalls you discuss.

>> 2.4 We agree this would provide some value; however, we prefer to avoid citing the studies because this might be not well received by some authors of these studies. In addition, despite their limitations, most of these studies have made other positive contributions to the field. <<

(4) On page 10369, line 13, I would change “realistic” to something else as it is simply an even distribution of defoliation/mortality over the duration of insect activity. It is arguably better than having it all occur at the end of the year, but is still not “real.”

>> 2.5 We replaced “realistic” with “approximated”. We also deleted “realistically” on p10373, 112, which was used with a similar meaning. <<

(5) Page 10369, lines 22 through 25, the authors state that the host DVLSM is in charge of the “resulting consequences for vegetation coexistence...”, however MIM requires user-input of % mortality. This seems to be contradictory.

>> 2.6 We thank you for raising this apparent contradiction. What we meant is that the host DVLSM simulates the post-mortality competition among the different PFTs present in the grid cell (instead of

MIM also prescribing the resulting impact on vegetation composition). Consequently, we modified the sentence as follows (modifications in italics and strikethrough): “The underlying philosophy of MIM is to prescribe only the direct damage to the vegetation caused by insect activity, letting the host DVLSM quantify the resulting consequences for *the post-mortality competition among the different vegetation types-vegetation coexistence* and the exchanges of carbon, energy, water, and momentum, based on the new conditions in the grid cells affected.” Please also note that MIM would not actually need to prescribe defoliator-caused mortality for DVLSMs that simulate PFT mortality explicitly (see our response 2.1). <<

(6) *Could you please explain how IBIS simulates vegetation competition in your section on IBIS? You bring it up later in the manuscript so it may be good to explain it here.*

>> 2.7 We thank you for suggesting this relevant addition. We included the following explanation (p10370, 125): “Competition among PFTs accounts for the two-strata structure of vegetation (i.e., trees capture light first, but grasses have preferential access to water as they have a higher proportion of their roots in the upper soil layers) and is based on the annual carbon balance of each PFT.” <<

(7) *Page 10372 and Appendix B2: You state that the updates to the leaf-to-canopy scaling integral and the removal of the “extpar” simplification affect canopy transpiration. How and in what direction?*

>> 2.8 We brought these modifications to IBIS before coupling it to MIM in order to improve carbon cycling in IBIS, and reported these changes here as this is the first manuscript we submit with this modified version of IBIS. Please note that we did not explicitly assess the effects of these changes on transpiration; however, these changes are directly related to the changes in net primary productivity (NPP) that we did assess. We performed various simulations for three transects: one in the boreal forest of North America, one in a drier region of North America, and one in the Amazon forest. In a nutshell, we found that the direct effect of these changes was to generally reduce NPP, with this reduction becoming greater as the level of CO₂ increased. Consequently, we concluded that “these changes reduced the strength of CO₂ fertilization in IBIS” (p10372, 15); please note that CO₂ fertilization in version 2 of IBIS was previously reported to be substantially higher than in other models (Cramer et al., 2001; McGuire et al., 2001; Friedlingstein et al., 2006). Our assessment also showed that the indirect consequences of these changes (e.g., changes in vegetation composition resulting from the changes in NPP, which differed among PFTs) could be substantial, with cascading impacts on carbon cycling and others. Although interesting, we believe that these elements are much too detailed to be discussed in the current manuscript and consider it more advisable to only report the main outcome mentioned previously (i.e., the direct effect is to reduce the strength of CO₂ fertilization). <<

(8) *Page 10373, line 1, delete “per se” as MIM does not model insect population dynamics nor does it include process-based methods of simulating the effects of them.*

>> 2.9 Done. <<

(9) *Page 10374, line 15 “Note that for...”: this sentence is confusing.*

>> 2.10 We are sorry that this sentence was not sufficiently clear. We entirely rephrased it as: “The duration of leaf onset simulated by IBIS is much shorter than duration_{IFT} for IFT #1, so there is no risk that this defoliator of deciduous trees will consume leaves faster than their simulated onset”. <<

(10) Page 10375, line 10. Why do you kill defoliated trees “suddenly” at the end of the year rather than throughout the year? You spent a good deal of time in the Introduction discussing “sudden” deaths as unrealistic, could you provide a justification here for your decision to use it for IFTs #1 and #2?

>> 2.11 We thank you for raising this point. We mentioned in the Introduction that “previous studies lacked realism by representing insect damage as end-of-year instantaneous events (instead of simulating their unfolding over many weeks during the growing season)” (p10369, 11). There is no major contradiction between this statement and the way we represented defoliators (i.e., IFTs #1 and #2) in MIM, because in the case of defoliators the unfolding damage during the growing season consists primarily of defoliation itself. Please also note that 100% defoliated trees (if no reflush is allowed) actually behave as dead standing trees (DSTs), because they can no longer perform photosynthesis or transpire. We clarified this point by adding the following sentence (p10375, 113): “Note that PFTs entirely defoliated by IFTs #1 or #2 behave exactly as dead trees if no reflush is allowed (see below), even if these killed PFTs are not labelled as “dead” before the end of the year.” <<

(11) Page 10375, line 20. Change “meanwhile” to “currently”

>> 2.12 Done. <<

(12) Page 10375, lines 23 and 24: Could you provide a justification for not quantifying the stem C consumed by IFT #3 and IFT biomass, and whether/how this may affect your results?

>> 2.13 The main reason was that we did not find the required data on the typical amount of stem C consumed by the mountain pine beetle (MPB) and on the partitioning of this consumed carbon among respiration, frass, and biomass. This affects our results by changing the CO₂ fluxes resulting from the activity of IFT #3, because: 1) we neglect the instantaneous release of CO₂ caused by respiration from IFT #3; 2) we do not account for the export of IFT #3 biomass out of the killed trees (which would reduce the amount of stem biomass available for decomposition later on); and 3) we do not account for the possibly different (likely higher?) rate of decomposition for IFT #3 frass versus tree litter. (Note that this third limitation also applies to frass from IFT #1 and #2, as it is treated as litterfall from leaf or needle by IBIS; p10375, 118). Nonetheless, the quantitative impact of these elements on our results is very small and much lower than other sources of uncertainty, because the total biomass of MPB required to kill a tree is orders of magnitude lower than the biomass of this tree. For example, it takes less than 600 individuals of the MPB to kill a tree (Jackson et al., 2008), with the efficiency of the attack strongly saturating when the attack density is ~3 times higher (Raffa and Berryman, 1983); a value of 1800 individuals is therefore an overestimate for a typical successful attack. Combined with a dry biomass of about 3.5 mg per individual (Reid and Purcell, 2011; Graf et al., 2012), this gives a total biomass (dry weight) of 6.3 g for MPB successfully attacking a tree. At such high density, a productivity of 10 pupae per MPB is optimistic (Raffa and Berryman, 1983); assuming that all pupae survive to emerge as adults (optimistic once again), this gives an upper bound of 63 g for the total biomass exported out of a killed tree, leading to a net export of 56.7 g (63 g minus 6.3 g). Now, the

average volume of a tree killed by MPB is around 0.57 m³ (Koot and Hodge, 1992; Jackson et al., 2008); using data for lodgepole pine in Canada, this means a dry biomass for stem (with bark and branches) of about 240 kg (CFS, 2015), i.e., more than 4,000 times higher than the total MPB biomass exported (for an assessment that overestimated on purpose the typical value of this export). Consequently, we consider that this simplification is not consequential in the context of our study and added the following precision to the text (modifications in italics): “At present, MIM does not quantify the stem carbon consumed by IFT #3 and the resulting IFT biomass; *given the difference between the total biomass of bark beetles and the biomass of the trees they killed, this should have very small impacts on the simulated carbon fluxes.*” <<

(13) *I am in general confused about how your model calculates % defoliation and % reflush? Is the % reflush for a day calculated based on the % of total leaf biomass lost up to that point, or something else? And does defoliation and reflush occur concurrently on a single day, and if so, which comes first in your simulation? Does the forest lose leaves to insects and then grow some back in the same day?*

>> 2.14 We are sorry about this confusion: Table 1 implicitly provided the response, but we should have included it in the text. Reflush, which can happen following defoliation by IFT #1 only, necessarily starts much after defoliation is completed (i.e., defoliation ends 35 days after leaf onset, whereas reflush starts 56 days after leaf onset); hence, reflush is indeed calculated based on the total amount of leaf biomass lost to defoliation. We therefore modified the text as follows (p10376, 13; modifications in italics and strikethrough): “[...] where total_{reflush} is the total amount of leaf ~~reflush~~ (in % of the *total* leaf biomass lost to defoliation *earlier in the same year*), duration_{reflush} is the duration of the ~~reflush~~ (in days), and start_{reflush} is the specific day of the year when ~~reflush~~ starts (see Table 1; *please note that reflush starts after defoliation is completed.*)” <<

(14) *Your snagfall dynamics for Case #5 seem incorrect. It is my understanding that lodgepole pine trees infested with MPB retain their leaves a year or more, and then they gradually fall over 4-7 years (Hansen 2013, Forest Science 60(3); Klutsch et al. 2009, Forest Ecology and Management 258). In Table 2 it shows there being no delay in litterfall for Case #5. Could you justify or explain this difference?*

>> 2.15 This discrepancy appears to reflect spatial differences in needlefall following death, as the 4-7 years duration mentioned in the review of Hansen (2014) and the primary research article of Klutsch et al. (2009) are for Colorado, whereas our main reference on this element (Wulder et al., 2006) is for British Columbia, Canada. This last reference actually reported that trees reach the gray stage (i.e., are needleless) ~31 months after the attack, whereas in MIM this happens ~40 months after the attack (e.g., on December 31, 2004 for an attack happening in 2001, which would last from August 1st to September 19th in MIM; see our Table 1). We note that other studies in Wyoming reported that trees were in the gray stage as soon as 3 or 4 years after the outbreak (Griffin et al., 2011; Simard et al., 2011). Regarding the absence of delay in litterfall following mortality, we also note that while Klutsch et al. (2009) did not find statistically significant differences in **total** litter depth between undisturbed stands and stands infested 0-3 years before, Griffin et al. (2011) reported statistically significant differences in total litter depth between undisturbed stands and stands disturbed 2 years before, while Simard et al. (2011) reported statistically significant differences in **needle** litter depth (more relevant than total litter depth) between undisturbed stands and stands disturbed 1-2 years before. Unfortunately, we are not aware of actual measurements of changes in needlefall per se, or at least of changes in needle litter mass (which would be more appropriate than litter depth to parameterize the rate of

needlefall). To address this issue of spatial variability, we added the following sentence at the end of the section presenting MIM (p10377, 122): “Moreover, for large-scale studies, the IFT- and DST-related parameters could vary spatially to reflect within-species variation, instead of having uniform values as we have used here (e.g., needlefall for Case #5 could occur over more than three years).” <<

(15) Could you justify your decision to prescribe a single, 100% mortality event occurring in one year? It does not seem realistic for 1) an entire lodgepole pine stand to be killed by MPB, especially the small stems, which are rarely infested by bark beetles (Pfeiffer et al. 2010, Global Change Biology 17; Veblen et al. 1994, Journal of Ecology 82(1)), and 2) that if this did occur, it would occur all in one year.

>> 2.16 We agree that it is not typical for 100% of pines to be killed by MPB, although this has been reported to happen (Hawkins et al., 2013). Please also note that IBIS, like many DVLSMs, does not have an intrinsic horizontal resolution (i.e., the model specifies the size of the vertical dimension only, for example, the height of trees); hence, IBIS-MIM results do not necessarily correspond to an entire stand, but could apply to a smaller ‘patch’ containing trees all killed in the same year. Nonetheless, we agree that prescribing a single, 100% mortality event was a simplification; we did it to increase the signal-to-noise ratio of our results, avoid having to consider the specific effect of more complex outbreak patterns, and test the theoretical upper limit to what could occur. In the context of our qualitative comparison of IBIS-MIM results with previous studies, we believe that this simplification was not misleading. For example, a previous study on MPB using a model similar to IBIS found that, for the same level of total mortality, the duration of the outbreak had a noticeable effect on net ecosystem productivity in the short term only (Edburg et al., 2011). We thus added the following sentence to justify this simplification (p10378, 118): “This single, 100% mortality event does not aim to represent actual MPB outbreaks, but was implemented for the sake of simplicity, to increase the signal-to-noise ratio of the results, and to test the theoretical upper limit of impacts.” <<

(16) Page 10379, line 19. It seems more likely that the MPB outbreak delayed the decline in lower canopy NPP rather than prevented it. As the decline occurred 600 to 750 years into the control/non-outbreak simulation, it may occur between years 1000 and 1150 of your outbreak simulation, which you do not show. Because the NE PFT retained its pre-outbreak levels of NPP by the end of your simulation, it seems that this may result in a decline in lower canopy NPP.

>> 2.17 We thank you for this insightful observation. Indeed, we have looked at results for the central grid cell over a longer time period and have found a decline in lower canopy NPP around year 1100 (followed by a recovery afterwards). These results, as well as the replicate simulations we performed under different weather conditions (p10385, 11), all suggest that decreases in lower canopy NPP (possibly followed by recoveries) are ‘bound to happen’ in the climate of the central grid cell. Consequently, we modified the text as follows (modifications in italics and strikethrough): “whereas the MPB outbreak released the lower canopy and ~~postponed-prevented~~ this decline, *which seems ‘bound to happen’ in the long term*”. <<

(17) Page 10379, line 26: Based on Figure 2, it seems that total NPP for the southern grid cell only declined initially (i.e. before year 100). At year 1000 it looks like the change in NPP between the outbreak and control is 0 or very close to it.

>> 2.18 We thank you for noticing this lack of precision in our previous explanation. We consequently improved the text, which now reads (modifications in italics and strikethrough): “In the southern grid cell, on the other hand, total NPP was reduced *for about 75 years and then increased marginally for a few decades, before returning to the control level* ~~except for a marginal increase ~ 100 years after the outbreak~~ (Fig. 2f).” <<

(18) I found the consequences of the standing dead trees very interesting. Your results show that it is important to include these dynamics in land surface models.

>> 2.19 We thank you for sharing this positive thought. We also believe that representing the physical presence of DSTs will likely lead to interesting insights about various land-atmosphere exchanges. <<

(19) Page 10382, line 14. Delete the phrase about the increase in shrub biomass being “akin to ‘not statistically significant’ ” as you do not include statistical tests in your study.

>> 2.20 We deleted this part of the sentence, which now reads (modifications in italics and strikethrough): “Note that the simulated increase in shrub biomass was *marginal* ~~very small~~ in the three grid cells, ~~akin to “not statistically significant” results in empirical studies,~~ but that grass biomass increased substantially.” <<

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Implementation of a Marauding Insect Module (MIM, version 1.0) in the Integrated Biosphere Simulator (IBIS, version 2.6b4) Dynamic Vegetation–Land Surface Model

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Abstract

Insects defoliate and kill plants in many ecosystems worldwide. The consequences of these natural processes on terrestrial ecology and nutrient cycling are well established, and their potential climatic effects resulting from modified land–atmosphere exchanges of carbon, energy, and water are increasingly being recognized. We developed a Marauding Insect Module (MIM) to quantify, in the Integrated Biosphere Simulator (IBIS), the consequences of insect activity on biogeochemical and biogeophysical fluxes, also accounting for the effects of altered vegetation dynamics. MIM can simulate damage from **broadleaf defoliators, needleleaf defoliators, and bark beetles**, three different insect functional types: (1) defoliators on broadleaf deciduous trees; (2) defoliators on needleleaf evergreen trees; and (3) bark beetles on needleleaf evergreen trees; with the resulting impacts being estimated by IBIS based on the new, insect-modified state of the vegetation. MIM further accounts for the physical presence and gradual fall of insect-killed dead standing trees. The design of MIM should facilitate the addition of other insect types besides the ones already included and could guide the development of similar modules for other process-based vegetation models. After describing IBIS-MIM, we illustrate the usefulness of the model by presenting results spanning daily to centennial timescales for vegetation dynamics and cycling of carbon, energy, and water ~~following a simulated outbreak of~~ in a simplified setting and for bark beetles only. More precisely, we simulated 100% mortality events from the mountain pine beetle for three locations in western Canada. We then show that these simulated impacts agree with many previous studies based on field measurements, satellite data, or modelling. MIM and similar tools should therefore be of great value in assessing the wide array of impacts resulting from insect-induced plant damage in the Earth system.

1 Introduction

The damage to plants caused by insects, particularly during outbreaks defined by sudden and major changes in insect population, are pervasive in

terrestrial ecosystems and affect not only vegetation dynamics, but also carbon, nutrient, energy, and water exchanges, and even atmospheric chemistry (Landsberg and Ohmart, 1989; Hunter, 2001; Lovett et al., 2002; Kurz et al., 2008; Amiro et al., 2008). Yet the simulation of insect-induced plant damage in climate models has lagged behind the simulation of fire, even though the two disturbance types were recognized as climate-related phenomena worthwhile of explicit representation in Dynamic Global Vegetation Models (DGVMs) more than 15 years ago (Fosberg et al., 1999).

Since the term “DGVM” is often used for interactive vegetation models that estimate only some of the exchanges of carbon, energy, water, and momentum with the atmosphere (Prentice et al., 2007; Quillet et al., 2010), we will refer here to the subset of DGVMs that compute all required land–atmosphere exchanges while accounting for dynamic vegetation as Dynamic Vegetation–Land Surface Models (DVLSMs) to prevent possible confusion ([e.g., many DGVMs do not compute the land-to-atmosphere fluxes of shortwave and longwave radiation](#)). Insect damage has been represented in DVLSMs in a handful of cases. Based on the empirical relationships of McNaughton et al. (1989), the ORganizing Carbon and Hydrology in Dynamic EcosystEms (ORCHIDEE) DVLSM accounts for background leaf consumption by herbivores (not limited to insects), but the realism of the resulting impact on simulated tree mortality has been questioned by the authors themselves (Krinner et al., 2005). The effects of prescribed mortality due to mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) outbreaks in western US on coupled carbon–nitrogen dynamics (Edburg et al., 2011) and water and energy exchanges (Mikkelsen et al., 2013b) have been studied in the Community Land Model (CLM) DVLSM. Medvigy et al. (2012) used the Ecosystem Demography version 2 (ED2) DVLSM to simulate the impacts of defoliation by the gypsy moth (*Lymantria dispar* Linnaeus) on vegetation coexistence and carbon dynamics in the eastern US. Background herbivory or insect outbreaks have also been simulated in DGVMs and other climate-driven terrestrial models (Randerson et al., 1996; Seidl et al., 2008; Wolf et al., 2008; Albani et al., 2010; Schäfer et al., 2010; Chen et al., 2015) less comprehensive than DVLSMs. However, most previous studies lacked realism by representing insect damage as end-of-year instantaneous events (instead of simulating their

unfolding over many weeks during the growing season) and/or by imposing the assumed consequences of insect activity (e.g., reduced total canopy conductance) rather than letting the model estimate these changes as a function of the new, insect-modified state of the vegetation. Moreover, many previous studies considered a single insect species, limiting their potential for global-scale studies, and failed to provide sufficient detail on the simulation of insect damage to efficiently guide modellers wanting to add insect disturbances to other DVLSMs.

Here, we present the “Marauding Insect Module” (MIM) we developed to simulate insect activity in DVLSMs and address the shortcomings identified above. MIM simulates insect activity with ~~a realistic~~ an approximated intra-annual schedule, prescribes only the plant damage caused directly by insects, and contains templates to allow for the inclusion of different insect functional types (IFTs). The concept of IFTs allows simplification of the huge diversity of insect species by grouping species that cause similar impacts (Cooke et al., 2007; Arneeth and Niinemets, 2010), and has recently been applied under the name of “Pathogen and Insect Pathways” in a simple ecophysiological model (Dietze and Matthes, 2014). We then illustrate, using MIM coupled to an existing DVLSM, the effects of a simulated MPB outbreak on many variables related to vegetation dynamics and exchanges of carbon, energy, and water, over daily to centennial timescales, and compare the results obtained to previous studies.

2 Model description

2.1 Overview

MIM was developed to be embedded within a host DVLSM and simulate the effects of insect activity on vegetation dynamics, and biogeochemical and biogeophysical exchanges. The underlying philosophy of MIM is to prescribe only the direct damage to the vegetation caused by insect activity, letting the host DVLSM quantify the resulting consequences for ~~vegetation coexistence~~ the post-mortality competition among the different vegetation types

and the exchanges of carbon, energy, water, and momentum, based on the new conditions in the grid cells affected. [Prescribing insect activity is less sophisticated than its prognostic simulation, but nevertheless allows relevant questions to be addressed concerning the climatic and ecological impacts of insect-caused plant damage.](#) We designed MIM so that it could be readily implemented in other DVLSMs in addition to the Integrated Biosphere Simulator (IBIS) we used in the current study. Furthermore, the structure of MIM is sufficiently flexible to allow for the representation of different insect species based on the templates we developed for three IFTs.

2.2 Integrated Biosphere Simulator (IBIS)

We provide here only a short description of IBIS and refer readers to Foley et al. (1996) and Kucharik et al. (2000) for more details. IBIS represents two vegetation canopies (trees in the upper canopy, shrubs and grasses in the lower canopy), multiple soil layers (six in this study, down to a depth of 4 m), and three snow layers when needed; both canopies intercept water and snow. Exchanges of radiation (shortwave and longwave), latent and sensible heat fluxes, and momentum between the atmosphere and the surface depend upon the state of each canopy. Water exchanges with the atmosphere consist of evaporation from intercepted water and the soil surface (including snow), as well as plant transpiration that is calculated consistently with photosynthesis and removes moisture from each soil layer according to an exponential root profile. Fluxes of heat and moisture between soil layers, with drainage at the bottom, are influenced by the soil texture class, which is provided as input data. A time step of 60 min is sufficient to update all fluxes and state variables in offline (i.e., not coupled to a climate model) simulations.

IBIS represents vegetation diversity through a limited set of plant functional types (PFTs) characterized by different climatic constraints and physiological parameters. Photosynthesis and autotrophic respiration are computed on the same time step as land surface physics (i.e., 60 min in this study) as a function of incoming radiation, CO₂ and O₂ concentration, temperature, and soil moisture stress. Changes in vegetation structure, including the proportions of competing PFTs, are determined at the end of each year, except for the leaf

phenology of deciduous PFTs that is updated daily. Competition among PFTs accounts for the two-strata structure of vegetation (i.e., trees capture light first, but grasses have preferential access to water as they have a higher proportion of their roots in the upper soil layers) and is based on the annual carbon balance of each PFT. Litterfall is estimated annually based on PFT-specific parameters for each biomass pool and partitioned into daily transfers to the soil over the following year. Carbon decomposition and transfers among the different soil pools, which are influenced by microbial biomass and soil temperature and moisture, are computed daily.

IBIS is arguably the first DVLSM to have been fully coupled to an Atmospheric General Circulation Model (Foley et al., 1998). Previous studies have shown that IBIS results compare reasonably well with observations, both over large regions (Foley et al., 1996; Kucharik et al., 2000; Lenters et al., 2000) and for field sites around the world (Delire and Foley, 1999; El Maayar et al., 2001, 2002; Kucharik et al., 2006). Model intercomparisons also demonstrated that IBIS results were similar to other DGVMs, except for a stronger CO₂ fertilization with version 2 of the model (Cramer et al., 2001; McGuire et al., 2001; Friedlingstein et al., 2006).

We downloaded source code for version 2.6b4 of IBIS from the Center for Sustainability and the Global Environment (SAGE) website (<http://nelson.wisc.edu/sage/data-and-models/lba/ibis.php>) with the required input data for climate (modified from the Climate Research Unit dataset CRU CL version 1.0 (New et al., 1999) by SAGE researchers for compatibility with IBIS) and for soil texture (based on an International Geosphere-Biosphere Program (IGBP) global dataset). The climate input data consist of different variables related to temperature, humidity (including precipitation and cloud cover), and wind speed. These climate data, which were provided for each month at a spatial resolution of 0.5°, are temporally downscaled by a random weather generator built into IBIS to simulate daily and hourly variability (see Kucharik et al., 2000, for more details). We modified the IBIS code before performing the illustrative simulations in Canadian forests (see Sect. 3) as follows:

1. We replaced the IGBP global soil dataset with survey data from the Soil Landscapes of Canada, versions 2.1 and 2.2, provided by the Canadian Soil Information System (<http://sis.agr.gc.ca/cansis/nsdb/slc/index.html>).
2. We modified the soil spin-up procedure due to the long time needed to reach equilibrium in Canada, the new procedure now taking 400 years (see Appendix A).
3. We improved the leaf-to-canopy scaling procedure for photosynthesis and transpiration, by: (1) replacing a mathematical simplification with the exact expression; and (2) adjusting the code that was used for the scaling integral (see Appendix B). Although the current study used a constant CO₂ concentration, it is worth noting that these changes reduced the strength of CO₂ fertilization in IBIS.
4. We slightly increased (from 2.5 to 2.7 years) the mean carbon residence time for the needle pool of the boreal needleleaf evergreen PFT, which resulted in a better spatial distribution of the PFTs that exist in Canada, as well as a better succession dynamics among these PFTs when starting a simulation from bare ground.
5. We fixed an error in the random weather generator code that had previously prevented consecutive wet days from ever occurring.
6. We modified various elements related to energy exchanges: (1) we updated the near-infrared optical properties of the lower-canopy leaves, based on values from version 4.0 of CLM (Oleson et al., 2010); (2) based on empirical data (Wang and Zeng, 2008), we constrained the variation of snow albedo as a function of solar zenith angle; and (3) we decreased the visible and near-infrared snow albedo parameters (see Appendix C). Following these changes, IBIS results for land surface albedo over Canada better matched MODIS-based values, both with (Barlage et al., 2005) and without (MOD43B3-derived Filled Land Surface Albedo Product) snow cover.
7. We added a subroutine to confirm that the full annual carbon cycle, including the effect of MIM, balanced to a numerical precision of at least $1 \times 10^{-5} \text{ kg C m}^{-2}$.

2.3 Marauding Insect Module (MIM)

MIM aims to represent the effect of insect activity, from both outbreaking and non-outbreaking insect species, on the coexistence of different PFTs and the land–atmosphere exchanges of carbon, energy, water, and momentum. MIM does not currently simulate insect population dynamics ~~per se~~, hence user-prescribed damage levels on defoliation and mortality (both in %) are required each year for each grid cell. It is the user’s responsibility to ensure that prescribed damage levels over multiple years or grid cells are appropriate and that, for defoliators, prescribed vegetation defoliation and mortality are consistent with each other (e.g., a single 5 % defoliation event is very unlikely to result in 80 % mortality). For host DVLSMs that, like IBIS, do not represent many individuals of the same PFT, a 5 % defoliation event translates into 100 % of the trees losing 5 % of their leaf area; in other DVLSMs, this same 5 % defoliation event could be assigned differently, for example by removing 100 % of the leaf area from 5 % of the trees. For each year and grid cell, MIM then implements all the required MIM changes in vegetation characteristics. The only input data for MIM are the prescribed levels of annual insect-caused defoliation and mortality, and the only state variables of the host DVLSM directly modified by MIM are the biomass and litter pools (to conserve carbon, new variables tracking insects respiration and biomass must also be added to the host DVLSM; see below). In fact, for DVLSMs that, unlike IBIS, simulate PFT mortality explicitly (e.g., as a function of carbohydrates reserves), MIM would not need input data on prescribed mortality in the case of defoliators. We designed MIM to operate with a daily time step to ~~realistically~~ simulate the intra-annual unfolding of insect activity and the resulting impacts, without the undue complications that would have stemmed from a sub-daily time step. Nevertheless, MIM could be adjusted to work under a shorter or longer time step.

MIM can currently simulate the activity from three IFTs parameterized to represent major outbreaking insect species in forests of North America:

- IFT #1: based on the forest tent caterpillar (*Malacosoma disstria* Hübner) and the gypsy moth, can defoliate (daily damage) and kill (year-end damage) broadleaf deciduous (BD) trees.
- IFT #2: based on the eastern spruce budworm (*Choristoneura fumiferana* Clemens), can defoliate (daily damage) and kill (year-end damage) needleleaf evergreen (NE) trees.
- IFT #3: based on the MPB (i.e., a bark beetle), can kill (daily damage) NE trees without previous defoliation.

The user can prescribe damage from different IFTs to occur concurrently within the same grid cell, but for simplicity a given PFT cannot currently be targeted by more than one IFT. For each IFT, the daily damage (defoliation for IFTs #1 and #2, mortality for IFT #3) unfolds by the same amount each day over the pre-defined duration of insect activity, thereby reaching the user-prescribed value at the end of the annual period of insect activity. The daily damage level (damage, in %) for a specific day d is thus given by:

$$\text{damage}(d) = \begin{cases} \frac{\text{input}_{\text{user}}}{\text{duration}_{\text{IFT}}} & \text{if } \text{start}_{\text{IFT}} \leq d < \text{start}_{\text{IFT}} + \text{duration}_{\text{IFT}} \\ 0 & \text{otherwise} \end{cases} \quad (1)$$

where $\text{input}_{\text{user}}$ is the user-prescribed damage level for the year (in %), $\text{duration}_{\text{IFT}}$ is the duration of insect activity during the year (in days), and $\text{start}_{\text{IFT}}$ is the specific day of the year when insect activity starts.

Since MIM does not model insect population dynamics, we used fixed parameters for the values of $\text{start}_{\text{IFT}}$ and $\text{duration}_{\text{IFT}}$ (see Table 1 for values and corresponding literature sources), except for $\text{start}_{\text{IFT}}$ of IFT #1: in this case, the activity begins on the same day as the IBIS-simulated beginning of leaf onset for the target tree, in accordance with the degree of synchrony between these two events for broadleaf defoliators (Dukes et al., 2009; Foster et al., 2013). ~~(Note that for realistic climatic conditions, the IBIS-simulated~~ The duration of leaf onset simulated by IBIS is much shorter than $\text{duration}_{\text{IFT}}$ for IFT #1.1, so there is no

risk that this defoliator of deciduous trees will consume leaves faster than their simulated onset.)

In reality, the start and duration of annual insect activity depend upon the phenological development of insects, for example the ending of the annual dormancy period for diapausing insects. Similarly, the linear unfolding of insect activity (i.e., equal day-to-day damage over the entire duration; see Eq. 1) is a simplification that could be refined in future implementations of MIM; yet, it provides a reasonable approximation of the intra-annual progression of damage caused by the IFTs considered (Régnière and You, 1991; Cook et al., 2008; Hubbard et al., 2013). For example, although the individual feeding rate for the fifth and sixth larval instars of the eastern spruce budworm is much higher than for younger instars, the decreasing population density throughout summer leads to an approximately linear progression of total defoliation (Régnière and You, 1991).

Each day, the relevant biomass pools (leaves for IFT #1, needles for IFT #2, and all biomass pools for IFT #3) are decreased as a function of damage(d). More precisely, in IBIS-MIM damage(d) is multiplied by the “equilibrium values” (without insect damage) of the relevant biomass pools, and the result is then subtracted from the current value (on day d) of the relevant biomass pools. This approach was implemented here, because IBIS computes these “equilibrium values” at the end of the previous year, when updating vegetation structure and proportions of competing PFTs; in other DVLSMs, however, this specific element of MIM’s implementation might need to be adjusted. Besides daily defoliation, IFTs #1 and #2 can kill trees (also according to user-prescribed damage levels); when this happens, mortality of the PFT targeted by IFT #1 or #2 occurs as a one-time event at the end of the year. We explain below how MIM deals with trees killed during a given year, either through daily (IFT #3) or sudden (IFTs #1 and #2) simulated mortality. Note that PFTs entirely defoliated by IFTs #1 or #2 behave exactly as dead trees if no reflush is allowed (see below), even if these killed PFTs are not labelled as “dead” before the end of the year.

The carbon contained in leaves or needles consumed by IFTs #1 and #2 based on damage(d) needs to be accounted for to obey the conservation laws that form the basis of DVLSMs. Consequently, MIM divides all the defoliated carbon among three pathways: respired (i.e., immediately returned to the atmosphere as CO_2), excreted as frass that is

then treated as leaf/needle litterfall by IBIS, or stored in IFT biomass (see Table 1). This last variable will be very relevant if MIM is eventually expanded to simulate insect population dynamics; meanwhile currently, the biomass of defoliator IFTs is simply exported out of the simulation domain at the end of each year, and IBIS net ecosystem carbon balance accounts for this export, as well as IFT respiration. At present, MIM does not quantify the stem carbon consumed by IFT #3 and the resulting IFT biomass; given the difference between the total biomass of bark beetles and the biomass of the trees they killed, this should have very small impacts on the simulated carbon fluxes.

Many tree species can produce a second flush of foliage after an early-season defoliation event (Jones et al., 2004; Schäfer et al., 2010). We therefore allowed for the possibility of re-flush-reflush in MIM, as this phenomenon can substantially influence simulated land-atmosphere exchanges and vegetation competition. The amount of reflush (in %) occurring during day d is given by:

$$\text{reflush}(d) = \begin{cases} \frac{\text{total}_{\text{reflush}}}{\text{duration}_{\text{reflush}}} & \text{if } \text{start}_{\text{reflush}} \leq d < \text{start}_{\text{reflush}} + \text{duration}_{\text{reflush}} \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

where $\text{total}_{\text{reflush}}$ is the total amount of leaf re-flush-reflush (in % of the total leaf biomass lost to defoliation earlier in the same year), $\text{duration}_{\text{reflush}}$ is the duration of the re-flush-reflush (in days), and $\text{start}_{\text{reflush}}$ is the specific day of the year when re-flush-reflush starts (see Table 1; please note that reflush starts after defoliation is completed). Each day, the leaf biomass pool of the defoliated PFT is then increased based on the value of $\text{reflush}(d)$ and the total amount of defoliation before the re-flush-reflush. Although $\text{duration}_{\text{reflush}}$ is currently determined by phenology algorithms from IBIS, approaches based on empirical data could be implemented instead. The value of $\text{total}_{\text{reflush}}$ for the year can be set to zero to prevent unrealistic reflush when the defoliation level is very low, or when trees have already been weakened by previous defoliation events, or if mortality is also prescribed for the same year.

When mortality is prescribed, MIM also needs to account for the carbon remaining in IFT-killed trees, both for mortality simulated as a sudden event at the end of the year (IFTs #1

and #2) and for daily mortality (IFT #3). We therefore added a new feature to IBIS, whereby a PFT killed by an IFT instantaneously becomes a dead standing tree (DST) conserving the same carbon pools. DSTs interact with energy, water, and momentum exchanges in the same way as live PFTs (e.g., interception of precipitation and absorption of radiation), but do not transpire or contribute to canopy photosynthesis. The simplest approach to simulate the fate of DSTs would have been to transfer all their carbon to IBIS litter pools at the end of the year when mortality happens. However, this would cause unrealistically large and sudden changes in litterfall and canopy structure, because insect-killed trees initially remain standing and fall gradually on the forest floor. Consequently, the carbon contained in DST pools is progressively transferred to the appropriate litter pools based on a prescribed schedule. MIM currently offers five possible schedules corresponding to the snagfall dynamics of different tree species:

- Case #1: BD tree PFT killed by IFT #1, fate of DST based on trembling aspen (*Populus tremuloides* Michx.) in eastern Canada (Angers et al., 2010).
- Case #2: BD tree PFT killed by IFT #1, fate of DST based on trembling aspen in western Canada (Hogg and Michaelian, 2015).
- Case #3: NE tree PFT killed by IFT #2, fate of DST based on balsam fir (*Abies balsamea* (L.) Mill.) in eastern Canada (Angers et al., 2010).
- Case #4: NE tree PFT killed by IFT #2, fate of DST based on black spruce (*Picea mariana* (Mill.) BSP) in eastern Canada (Angers et al., 2010).
- Case #5: NE tree PFT killed by IFT #3, fate of DST based mostly on MPB-killed lodgepole pine (*Pinus contorta* var. *latifolia*) in western North America (Lewis and Hartley, 2005; Wulder et al., 2006; Griffin et al., 2011; Simard et al., 2011).

The transfer of carbon from DST pools (i.e., fine roots, leaves/needles, and stems, the latter including coarse roots and branches) towards IBIS litter pools starts after a delay period and then occurs at a specific rate. [note that the delay refers to the time of attack,](#)

even for Case #5. Table 2 gives the value of these parameters for the five cases currently implemented in MIM. In all cases, the DST fine roots are transferred to IBIS litter pools as a one-time event, at the end of the year of mortality (note that IBIS partitions all annual DST transfers into daily amounts over the following year). For deciduous PFTs (i.e., Cases #1 and #2), the transfer of DST leaves also occurs as a one-time event. On the other hand, the DST needles are transferred to litter pools over many years for evergreen PFTs (i.e., Cases #3–5). Finally, the DST stems are also transferred to litter pools over many years, usually starting after a 5-year delay period (see Fig. 1). As with the IFT-related parameters, all these aspects of DST dynamics can easily be modified as a function of new data or to accommodate other tree species. Moreover, for large-scale studies, the IFT- and DST-related parameters could vary spatially to reflect within-species variation, instead of having uniform values as we have used here (e.g., needlefall for Case #5 could occur over more than three years).

3 Illustration of IBIS-MIM performance

3.1 Simulation design

To illustrate the performance of IBIS-MIM, we conducted six simulations using the MPB-inspired IFT (i.e., IFT #3 from Table 1) with DST dynamics based mostly on MPB-killed lodgepole pine (i.e., Case #5 from Table 2). We performed an outbreak simulation and a control simulation in each of three different locations in British Columbia, Canada, henceforth designated as the northern, central, and southern grid cells (Table 3). These three locations, which we used as proxies to assess the influence of climate on the main outcomes, have suffered substantial MPB-caused mortality since 2000 (Walton, 2013). The mean annual temperature was almost equal in the northern and central grid cells, but summer was warmer and winter was colder in the former; the southern grid cell was warmer throughout the year. Annual precipitation was very similar in the three grid cells, but summer

rainfall was substantially lower in the southern grid cell, leading to lower soil water content during the growing season.

All simulations started with the new 400-year spin-up procedure and were performed under a constant climate. In each grid cell, we prescribed a single 100 % mortality event happening in year 401 (i.e., in year 1 following the spin-up period) and continued the simulation up to year 1000. This single, 100 % mortality event does not aim to represent actual MPB outbreaks, but was implemented for the sake of simplicity, to increase the signal-to-noise ratio of the results, and to test the theoretical upper limit of impacts. We used the same climate data and weather generation for the outbreak simulation and the no-mortality control simulation performed in a given grid cell. In addition to yearly results throughout the entire simulation, we saved daily (monthly) results during 10 (200) years after the mortality event. We excluded the boreal BD tree PFT from simulations due to the generally low density of such trees within MPB-attacked stands in British Columbia (Hawkins et al., 2012). Consequently, competition took place among four different IBIS PFTs: boreal NE trees (i.e., the target PFT), evergreen shrubs, cold-deciduous shrubs, and C₃ grasses.

3.2 Responses over different timescales

Figure 2 shows the effect of the single MPB outbreak on net primary productivity (NPP) in the three grid cells. In all cases, simulated NPP of the target NE trees decreased to zero while NPP of the lower canopy substantially increased following the 100 % mortality event; the productivity of the different PFTs then gradually resumed towards the pre-outbreak levels (Fig. 2a, c, and e). However, the growth release of the lower canopy was much stronger in the northern and central grid cells than in the southern grid cell, where conditions were drier during the growing season. Such positive impacts on lower canopy have often been reported following outbreaks from MPB and other bark beetles (Stone and Wolfe, 1996; Klutsch et al., 2009; Griffin et al., 2011; Simard et al., 2011; Bowler et al., 2012; Brown et al., 2012; Vanderhoof et al., 2014).

In the northern and central grid cells, the lower canopy growth release exceeded the productivity losses coming from the death of NE trees, so that total post-outbreak NPP

soon exceeded NPP in the control runs (Fig. 2b and d). The increase in Δ NPP in the central grid cell from year ~ 600 onwards came from the impact of the outbreak on the competition balance among PFTs: although NPP seemed relatively stable at the end of the spin up (i.e., years 300–400 in Fig. 2c), lower canopy NPP decreased markedly between years 600 and 750 in the control simulation, whereas the MPB outbreak released the lower canopy and ~~prevented this decline~~postponed this decline, which seems 'bound to happen' in the long term. Empirical (Romme et al., 1986; Belovsky and Slade, 2000) and modelling (Mattson and Addy, 1975; Seidl et al., 2008; Albani et al., 2010; Pfeifer et al., 2011; Hansen, 2014) studies of insect damage have previously shown that total productivity, biomass, or carbon storage can be higher in disturbed than in undisturbed ecosystems. As was the case in IBIS-MIM, the mechanisms identified in these previous studies involved responses from non-target vegetation, i.e., other species or non-attacked age classes of the target species. In the southern grid cell, on the other hand, total NPP was reduced ~~except for a marginal increase ~ 100 for about 75 years after the outbreak~~and then increased marginally for a few decades, before returning to the control level (Fig. 2f).

The previous results also exhibited an interesting feature: in all grid cells, the recovery of the NE trees was initially very rapid, but was then reversed after ~ 20 –25 years before re-summing again (Fig. 2a, c, and e). Although additional simulations would be required to confirm our hypothesis, we believe that this “dip” came from indirect biogeophysical interactions between recovering NE trees and decaying DSTs in the relatively cold climate considered here. After MPB mortality, the interception of radiation (shortwave and longwave) by DSTs warmed the surrounding air, allowing photosynthesis in the recovering NE trees to occur faster at a higher temperature than if DSTs had been absent. As DSTs gradually fell, NE trees captured more light but had a lower needle temperature, resulting in lower NPP. Such strong photosynthesis–temperature responses have been found to play a major role when simulating future vegetation dynamics (Sitch et al., 2008; Medvigy et al., 2010) and carbon cycle–climate feedbacks (Matthews et al., 2005).

Figure 3 shows the impact of the outbreak on four variables (two related to carbon cycling, one to energy exchanges, and one to water cycling) over different timescales (yearly,

monthly, and daily). The changes in net ecosystem productivity (NEP; Fig. 3a) were driven mostly by NPP, including the increases in total NPP \sim 5 years post-mortality in the northern and central grid cells. Changes in heterotrophic respiration (R_h) were generally smaller, but contributed to the NEP local minimum around year 25 (particularly visible in the central and southern grid cells) and progressively offset the NPP increase in the northern and central grid cells, so that Δ NEP became negligible after roughly a century. The total amount of aboveground litter (Fig. 3b) slightly decreased for a few years after the mortality event, because the total litterfall from DSTs in the outbreak simulations was initially lower than from live trees in the control simulations. After a few years, however, the situation was reversed and the increase in aboveground litter was $> 1.5 \text{ kg C m}^{-2}$ in all grid cells \sim 25 years after the mortality event, gradually decreasing afterwards. After about 75 years, the aboveground litter was lower in the outbreak simulations due to the reduced litterfall from the still recovering vegetation. The pre-outbreak equilibrium was reached about three centuries after the mortality event. The monthly albedo (Fig. 3c) increased during the initial years as the needles fell from DSTs. The impact of snow cover was clearly apparent in the yearly cycle of albedo changes, with much higher albedo increases during winter months. The few points showing a decrease in albedo resulted from the earlier snowmelt in the outbreak simulations, a response that is illustrated for the central grid cell (Fig. 3d). While the snow amount was slightly higher following the first snowfall events (barely visible in Fig. 3d), in the middle of winter the control grid cells generally had more snow. But above all the snowmelt started and finished much earlier in the outbreak simulations, by about three weeks in the case illustrated.

3.3 Evaluation of performance

Table 4 presents a qualitative comparison of IBIS-MIM outcome after an MPB-caused 100 % mortality event with the results from 37–38 different studies based on field measurements, satellite data, or modelling. Except for some of the works reviewed in Mikkelsen et al. (2013a), these studies all had actual control and effect results. Most studies assessed the impacts of mortality caused by MPB or other bark beetles, although a few studies depended

upon other disturbances (girdling or clearcutting) for the effect. We note, however, that the identification of appropriate control stands for field and satellite studies is not a straightforward task, which may partly explain why the qualitative impact (increase, no change, or decrease) of MPB mortality varied across studies for some variables. Furthermore, the level of stand mortality differed among studies or was not quantified and, except for a few modelling studies, was less than the 100 % mortality simulated in IBIS-MIM. These limitations prevented us from performing more quantitative comparisons.

The comparisons covered 28 different variables related to carbon cycling and vegetation dynamics, energy exchanges, and the water cycle. These comparisons further spanned various timescales: annual (all variables related to carbon cycling and vegetation dynamics, albedo, evapotranspiration, runoff, and soil moisture), seasonal/monthly (all variables related to energy exchanges, evapotranspiration, transpiration, soil moisture, snow depth/amount, and snowmelt onset), and daily (peak flow, snow depth/amount, and snowmelt onset). Among the 28 variables, IBIS-MIM prescribed only the snagfall dynamics of DSTs. IBIS-MIM results agreed with previous studies for most variables, thereby illustrating that the model constitutes an appropriate tool for studying the impacts of insect-induced plant damage on many inter-dependent variables spanning a large range of timescales.

For most variables related to carbon cycling and vegetation dynamics, the qualitative responses of IBIS-MIM changed over time for two reasons. First, as seen in Sect. 3.2, lower canopy biomass substantially increased following the canopy opening in the northern and central grid cells (but much less in the southern grid cell), eventually reversing the initial response for GPP, NPP, R_a , R_s , NEP, and total LAI (abbreviations are defined in Table 4) in these two locations ~ 5 –15 years after the MPB outbreak. Note that the simulated increase in shrub biomass was very small marginal in the three grid cells, **akin to “not statistically significant” results in empirical studies**, but that grass biomass increased substantially. Lower canopy fractional cover increased in the northern grid cell only, because this variable was already at its maximum value before the mortality event in the other two grid cells. Second, the prescribed snagfall dynamics of DSTs led to a carbon response over

multiple timescales (Edburg et al., 2011) that affected R_h , NEP, and aboveground litter (see also Fig. 3a and b).

Among the variables related to energy exchanges, IBIS-MIM responses for temperature and albedo systematically agreed with previous studies. (The air temperature in field studies was measured close to breast height, a level at which IBIS-MIM does not estimate temperature. As a proxy, we used the mean of the simulated temperature responses in the middle of the upper and lower canopies.) These responses became particularly strong and sustained after the complete fall of needles from DSTs. We note that the impacts on temperature variables in IBIS-MIM were generally opposite between winter and summer; unfortunately, none of the previous studies reported wintertime temperature changes. For latent and sensible heat fluxes, however, IBIS-MIM differed noticeably from previous studies: after the year of mortality, summertime latent heat flux actually increased for three years in the southern grid cell and for much longer in the other grid cells. The pattern was the opposite for summer sensible heat, except in the southern grid cell where this variable did not show a systematic behaviour. We think that these responses for summer turbulent heat fluxes had two different causes. For 1–4 years after the mortality event, the higher summer latent heat flux in all grid cells came from a major increase in evaporation which, in turn, probably resulted from the combination of two pre-existing biases in the land surface module (LSX) that computes the exchanges of energy, water, and momentum within IBIS-MIM: (1) the overestimation of upper soil temperature in summer (El Maayar et al., 2001), which likely increased following the mortality event; and (2) the overestimation of heat storage within stems (including DSTs in our simulations), leading to an overestimated nighttime evaporation flux when the heat is released (Pollard and Thompson, 1995; El Maayar et al., 2001). For ≥ 5 years after the mortality event, the increase in summer latent heat flux in the northern and central grid cells rather resulted from the strong growth of grasses mentioned previously. Indeed, NPP and LAI of grasses in these grid cells were then large enough to overcompensate for the decreases due to tree mortality, resulting in higher total transpiration, evapotranspiration, and latent heat flux. In the southern grid cell, where the response from grasses was much smaller, summer latent heat flux decreased ≥ 5 years post-mortality.

While acknowledging possible issues with these IBIS-MIM results, particularly 1–4 years post-mortality, we want to underline the limitations from previous studies on turbulent heat fluxes and the closely related evapotranspiration. Three of the four modelling studies (Wiedinmyer et al., 2012; Mikkelsen et al., 2013b; Chen et al., 2015) indirectly “forced” the responses they obtained by directly reducing the total canopy conductance without accounting for the possible growth release of the surviving vegetation, while the fourth modelling study (included in the Mikkelsen et al., 2013a, review) only computed the change in runoff and then assumed no change in soil moisture to estimate the change in evapotranspiration. The two satellite-based studies rest upon the highly-parameterized MODIS evapotranspiration dataset (Mu et al., 2011), which has not been developed and tested in the context of MPB-killed forests. The only field-based study on evapotranspiration (included in the Mikkelsen et al., 2013a, review) also neglected possible changes in soil moisture. Furthermore, other field-based studies – not included in our comparison due to their lack of control data – found very little change in evapotranspiration over various years following MPB mortality for sites located close to the northern grid cell (Bowler et al., 2012; Brown et al., 2014), or found that evapotranspiration increased over three years despite an ongoing increase in MPB mortality at a site in Wyoming, US (Reed et al., 2014).

For water cycle variables besides evapotranspiration, the agreement with previous studies was also fairly good. The soil water budget in IBIS-MIM is very sensitive to the distribution of precipitation events during each month, so the responses were highly variable for runoff, peak flow, and soil moisture, particularly in the southern grid cell. Nevertheless, the responses provided in Table 4 were observed over the first ~ 5 years. Afterwards, runoff remained higher in the outbreak simulation for the southern grid cell (resulting in part from the faster snowmelt), but became smaller in the other grid cells due to the increase in evapotranspiration as leaf area expanded. A field study on drought-induced tree mortality also linked an unexpected decrease in annual runoff to a growth release of the lower canopy (Guardiola-Claramonte et al., 2011). Peak flow, on the other hand, remained overall higher in all grid cells for at least a decade. After an initial increase lasting ~ 5 years, soil moisture showed a sustained decrease, likely caused by the snowmelt-related higher runoff in

the southern grid cell and by the higher evapotranspiration in the other grid cells. Although generally often slightly higher at the beginning of the season, snow depth/amount overall decreased in IBIS-MIM (see Fig. 3d), contrary to most previous studies. This outcome likely resulted from the overestimated heat storage in DSTs and could lead to the simulated snow cover season ending too early. Yet areal snow coverage, which matters most for albedo, was equal for the control and outbreak simulations during most of the snow cover season and, most importantly, the earlier onset of snowmelt agreed with the majority of previous studies and was of reasonable magnitude.

We checked whether the outcomes presented in Table 4 were sensitive or not to the specific weather simulated by performing two additional replicates for each grid cell. We found that the qualitative outcomes were the same for all variables, except for one minor difference: for one of the two replicates in the central grid cell, the post-outbreak fractional cover of the lower canopy increased slightly because it was not already at its maximum value, contrary to the case reported in Table 4. The quantitative results were also very similar across replicates, except for some water-related variables that are very sensitive to the exact timing of precipitation events.

Finally, although assessing IBIS was not the point of this study and has already been done elsewhere (Foley et al., 1996; Delire and Foley, 1999; Kucharik et al., 2000, 2006; Lenters et al., 2000; El Maayar et al., 2001, 2002), the results obtained for the three grid cells compared favourably to recent studies, with a small underestimation of biomass (Beaudoin et al., 2014) and NPP (Gonsamo et al., 2013). Obtaining reliable data on soil carbon is notoriously difficult; when compared to the Harmonized World Soil Database (down to a depth of 1 m) as provided by Exbrayat et al. (2014), IBIS apparently overestimated soil carbon (down to a depth of 4 m), at least in the southern grid cell, even when accounting for the fact that a substantial fraction of soil carbon is found at a depth greater than 1 m (Jobbágy and Jackson, 2000).

4 Discussion

Many previous studies have represented insect damage in DVLSMs or less comprehensive climate-driven terrestrial models (Randerson et al., 1996; Krinner et al., 2005; Seidl et al., 2008; Wolf et al., 2008; Albani et al., 2010; Schäfer et al., 2010; Edburg et al., 2011; Medvigy et al., 2012; Mikkelsen et al., 2013b; Chen et al., 2015). To our knowledge, however, our study is the first to assess, over daily to centennial timescales, the impacts from insect damage on vegetation dynamics and the carbon, energy, and water cycles in an integrated way (see Sect. 3). We compared the qualitative impacts of a simulated MPB outbreak on 28 IBIS-MIM variables with many field-, satellite-, and modelling-based studies (see Table 4), finding an overall good level of agreement. Our results further suggest that the physical presence of DSTs can benefit vegetation regrowth due to their interactions with radiation. A previous study also showed that falling DSTs can impact tree recovery through altered soil nitrogen dynamics (Edburg et al., 2011). Since DSTs contribute substantially to the biogeophysical and biogeochemical legacies of insect outbreaks, they should be explicitly modelled when feasible.

We developed MIM to account for the major processes related to insect activity (Table 1), including the dynamics of DSTs (Table 2) when applicable. The generic design of the module could serve as a template to represent other IFTs and/or DSTs, and should facilitate future developments such as replacing the prescribed intra-annual unfolding of insect activity with algorithms based on simulated insect phenology. Moreover, MIM could be [modified by simulating the fall of DSTs probabilistically \(e.g., as in FireBGCv2; Keane et al., 2011\)](#) or enhanced by: simulating the fall of DSTs as a function of environmental conditions (Lewis and Hartley, 2005) [or the size of DSTs \(e.g., as in FVS; Rebain et al., 2010\)](#); reducing snow albedo when needles fall from DSTs (Pugh and Small, 2012); and accounting for changes in needle optical properties as they turn from green to red (Wulder et al., 2006).

The simple structure of MIM should also facilitate the adaptation of the module to other DVLSMs. Of course, MIM will then reflect many of the strengths and weaknesses of its host model. For example, the parameters of the boreal NE PFT in IBIS 2.6b4 were not based on

lodgepole pine specifically. Furthermore, IBIS simulates a single boreal NE PFT, whereas different NE tree species can coexist in MPB-attacked stands (Hawkins et al., 2012). Since IBIS does not represent different age cohorts within the same PFT, the model cannot account for the fact that MPB generally targets the larger trees (Axelson et al., 2009; Hawkins et al., 2012; Hansen, 2014). For < 100 % mortality, the responses of surviving younger trees would likely differ from those of surviving mature trees and could enhance the recovery of the target species. Impacts on tree demographics might also lead to complex stand-level responses, for example increasing total biomass despite reduced productivity because of a strong decrease in competition mortality (Pfeifer et al., 2011). Other shortcomings of IBIS that affected IBIS-MIM results came from the apparent overestimation of stem heat storage (Pollard and Thompson, 1995; El Maayar et al., 2001) and the absence of carbon–nutrient interactions (Edburg et al., 2011, 2012; Mikkelsen et al., 2013a). On the other hand, IBIS two-strata vertical vegetation structure and detailed biophysics computations, both inherited directly from the LSX land surface module (Pollard and Thompson, 1995), allowed the lower canopy growth release and the biogeophysical impacts of DSTs presence to be simulated more realistically than with many other DVLSMs.

Finally, the strong link between climate and insect life cycles (Dukes et al., 2009; Bentz et al., 2010) provides incentive for eventually enhancing MIM by including process-based representations of insect population dynamics in DVLSMs (Fosberg et al., 1999; Arneth and Niinemets, 2010), rather than prescribing insect damage through input data.

5 Conclusions

Insect damage to vegetation triggers major interacting effects on the cycles of carbon, nutrients, energy, and water, and also affects atmospheric chemistry (Amiro et al., 2010; Arneth and Niinemets, 2010; Clark et al., 2010, 2012; Bowler et al., 2012). Given that Dynamic Vegetation–Land Surface Models (DVLSMs) were designed to simulate coupled biogeophysical and biogeochemical fluxes within a consistent framework that accounts for changes in vegetation state, these models appear as good candidates to

assess many of the consequences from insect-induced vegetation damage over a wide range of timescales.

Here, we presented version 1.0 of the Marauding Insect Module (MIM) developed to simulate, within the Integrated Biosphere Simulator (IBIS) DVLSM, the impacts of prescribed levels of annual insect damage. MIM currently includes three insect functional types (IFTs) broadly representing defoliators of broadleaf trees, defoliators of needleleaf trees, and bark beetles. The parameterization of IFTs was based on key outbreaking insects affecting North American forests, but could be modified to represent other insect species ~~and probably, with additional adjustments,~~ effects on other vegetation types (e.g., agricultural fields), and, with further adjustments, effects of some vegetation pathogens (e.g. [Dietze and Matthes, 2014](#)). Similarly, the fate of the insect-killed dead standing trees (DSTs) can easily be adjusted to go beyond the five cases currently implemented. Finally, MIM itself was designed in such a way that it should be transferable to other DVLSMs with limited adjustments.

We also illustrated the realism and usefulness of IBIS-MIM by simulating a 100% mortality event caused by the mountain pine beetle at three locations within British Columbia, Canada. First, we looked at the impacts of the outbreak on a variety of processes spanning daily to centennial timescales. One interesting outcome from this assessment is that DSTs intercept radiation and therefore warm the surrounding air, which in a cold climate could be beneficial for tree recovery. Second, we found that IBIS-MIM agreed qualitatively with the results from ~~over 30~~ 38 field-, satellite-, and model-based studies for 28 different variables related to vegetation dynamics, and exchanges of carbon, energy, and water. These outcomes supported the idea that DVLSMs are valuable tools to study the consequences from insect-induced plant damage.

Insect outbreaks, but also less spectacular background-level vegetation damage caused by insects, are part of the natural dynamics of terrestrial ecosystems worldwide. The use of IBIS-MIM and other similar process-based modelling tools suitable for climate-related studies should therefore help us better understand the wide range of possible impacts of insects on several processes in the Earth system, for past, current, and future conditions.

Code availability

The code for IBIS-MIM (in Fortran 77) is available upon request from the corresponding author or through the following link: <http://landuse.geog.mcgill.ca/~jean-sebastien.landry2@mail.mcgill.ca/ibismim/>. [IBIS-MIM requires the NetCDF utilities \(http://www.unidata.ucar.edu/software/netcdf/\)](http://www.unidata.ucar.edu/software/netcdf/) for input and output data handling.

Appendix A: Soil spin-up procedure

The previous soil spin-up procedure lasted 150 years and was performed as follows: 40 iterations of the soil module were repeated each year during the first 75 years; then, during the following 25 years, the number of iterations per year decreased linearly from 40 to 1; and finally, during the last 50 years, soil carbon pools were brought to equilibrium under a single iteration per year. The total number of soil module iterations under this procedure was around 3500.

The new soil-spin up procedure lasts 400 years and is performed as follows: 80 iterations of the soil module are repeated each year during the first 350 years; then, during the following 40 years, the number of iterations per year decreases linearly from 80 to 1; and finally, during the last 10 years, soil carbon pools are brought to equilibrium under a single iteration per year. The total number of soil module iterations under this procedure is around 29 600.

Appendix B: Leaf-to-canopy scaling

B1 The “extpar” simplification

The net photosynthesis ($A_n(X)$, in $\text{mol CO}_2 \text{ s}^{-1} \text{ m}^{-2}$ of leaf) for a leaf that is X units into the upper or lower canopy (where X is the cumulative vegetation (leaf plus stem) area index,

in m^2 of vegetation m^{-2} of ground, with $X = 0$ at the top of the canopy) is computed as:

$$A_n(X) = A_n(0) \frac{A \exp(-kX) + B \exp(-hX) + C \exp(hX)}{A + B + C} \quad (B1)$$

where $A_n(0)$ is the photosynthesis for a leaf at the top of the canopy and A , B , C , k , and h are coefficients computed in IBIS. Previously, this expression was simplified to:

$$5 \quad A_n(X) = A_n(0) \exp(-\text{extpar}X) \quad (B2)$$

with:

$$\text{extpar} = \frac{Ak + Bh - Ch}{A + B + C} \quad (B3)$$

Now, Eqs. (B2)–(B3) are not equal to Eq. (B1) unless kX and hX are both very small. We therefore worked directly with Eq. (B1) and removed the “extpar” simplification from the code. Note that this simplification might have been required in version 1 of IBIS, which
 10 used a different leaf-to-canopy scaling approach than version 2 (Foley et al., 1996; Kucharik et al., 2000).

B2 Leaf-to-canopy scaling integral

The total canopy photosynthesis ($A_{n,\text{canopy}}$, in $\text{mol CO}_2 \text{ s}^{-1} \text{ m}^{-2}$ of ground) is given by the
 15 following scaling integral:

$$A_{n,\text{canopy}} = \frac{\text{LAI}}{\text{XAI}} \int_0^{\text{XAI}} A_n(X) dX \quad (B4)$$

where LAI is the total canopy leaf area index and XAI is the total canopy vegetation (leaf plus stem) area index. Previously, the LAI/XAI factor was removed from the integral above and was included in the computation of the photosynthetically active radiation absorbed by

leaves at the top of the canopy; the results for $A_{n,\text{canopy}}$ were then the same for light-limiting conditions, but not under Rubisco-limiting or CO_2 -limiting conditions. We therefore adjusted the code to work directly with Eq. (B4) under all conditions. Note that this adjustment and the removal of the “extpar” simplification affected canopy transpiration, which is computed as a function of canopy photosynthesis.

Appendix C: Energy exchanges

C1 Near-infrared optical properties of lower-canopy leaves

We modified the reflectance (unitless) from 0.60 to 0.40, and the transmittance (unitless) from 0.25 to 0.30.

C2 Snow albedo vs. solar zenith angle

IBIS increases snow albedo for solar zenith angles greater than 60° , but these increases appeared too large for very high zenith angles. We therefore limited these increases to a maximum of 10 % above the value at 60° for visible radiation and to a maximum of 15 % above the value at 60° for near-infrared radiation.

C3 Visible and near-infrared snow albedo parameters

We decreased the following parameters related to snow albedo (unitless): low-temperature value in the visible (from 0.90 to 0.80), high-temperature value in the visible (from 0.70 to 0.60), low-temperature value in the near-infrared (from 0.60 to 0.50), and high-temperature value in the near-infrared (from 0.40 to 0.30).

Code availability

The code for IBIS-MIM (in Fortran 77) is available upon request from the corresponding author or through the following link: [IBIS-MIM requires the NetCDF utilities \(\) for input and output data handling.](#)

Author contributions. J.-S. Landry developed MIM and modified IBIS with advice from D. T. Price, N. Ramankutty, and L. Parrott; J.-S. Landry performed the simulations with IBIS-MIM and analyzed the results; J.-S. Landry prepared the manuscript with contributions from all co-authors.

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Table 1. Parameters for the insect functional types (IFTs) currently represented in MIM (see Eqs. 1–2 for $\text{start}_{\text{IFT}}$, $\text{duration}_{\text{IFT}}$, $\text{start}_{\text{reflush}}$, $\text{total}_{\text{reflush}}$, and $\text{duration}_{\text{reflush}}$); n/a: not applicable.

| Element | IFT #1 | IFT #2 | IFT #3 |
|--|---|-------------------------------------|-------------------------|
| $\text{start}_{\text{IFT}}$ | Leaf onset ^{a;1,2} | 1 May ^{3–5} | 1 August ^{6,7} |
| $\text{duration}_{\text{IFT}}$ | 35 days ^{8–10} | 60 days ^{3–5} | 50 days ¹¹ |
| Unfolding of IFT activity | Linear ^{b;8} | Linear ^{b;12} | Linear ^{b;11} |
| Fate of defoliated carbon ^c | (50) : (33) : (17) ⁸ | (70) : (20) : (10) ^{12,13} | n/a |
| $\text{start}_{\text{reflush}}$ | 56 days after leaf onset ^{14,15} | n/a | n/a |
| $\text{total}_{\text{reflush}}$ | 50 % of defoliation loss ¹⁵ | n/a | n/a |
| $\text{duration}_{\text{reflush}}$ | Typically ~ 5 days ^a | n/a | n/a |

¹ Dukes et al. (2009); ² Foster et al. (2013); ³ Royama (1984); ⁴ Fleming and Volney (1995); ⁵ Royama et al. (2005); ⁶ Safranyik and Carroll (2006); ⁷ Wulder et al. (2006); ⁸ Cook et al. (2008); ⁹ Couture and Lindroth (2012); ¹⁰ NRCan (2012); ¹¹ Hubbard et al. (2013); ¹² Régnière and You (1991); ¹³ Koller and Leonard (1981); ¹⁴ Jones et al. (2004); ¹⁵ Schäfer et al. (2010)

^a Determined by IBIS phenology algorithms. ^b Means that the daily damage (defoliation for IFTs #1 and #2, mortality for IFT #3) is the same throughout the annual duration of insect activity. ^c Given in %, as (IFT frass) : (IFT respiration) : (IFT biomass), the frass including the unconsumed leaves/needles and being treated as litterfall by IBIS.

Table 2. Parameters for the dynamics of dead standing trees (DSTs) currently represented in MIM.

| Element | Case #1 | Case #2 | Case #3 | Case #4 | Case #5 |
|----------------------------|-------------------------|-----------------------------------|------------------------------------|------------------------------------|-----------------------|
| Delay – fine roots | None ^a | None ^a | None ^a | None ^a | None ^a |
| Rate – fine roots | One-time ^a | One-time ^a | One-time ^a | One-time ^a | One-time ^a |
| Delay – leaves | None ^{a,b} | None ^{a,b} | None ^b | None ^b | None |
| Rate – leaves ^c | One-time ^{a,b} | One-time ^{a,b} | 3 years ^b | 3 years ^b | 3 years |
| Delay – stems | 5 years | None | 5 years | 5 years | 5 years |
| Rate – stems ^c | 20 years | 5 years (50 %) 10 years (50 %) | 10 years (17 %) 10 years (83 %) | 25 years (90 %) 15 years (10 %) | 20 years |

^a All transferred to litter on the year of mortality. ^b If some leaves/needles remain because mortality occurred with less than 100 % defoliation or reflush happened. ^c Rates are linear and start after the delay period; for stems, some cases have two consecutive linear periods showed on two lines: for each period, the duration (in years) and the total fraction transferred over the period (in %) are provided.

Table 3. Input climate data and soil texture for the three grid cells.

| Element | Northern | Central | Southern |
|---------------------------------------|------------|-----------|------------|
| Coordinates (degrees) | | | |
| Latitude | 55.25° N | 52.75° N | 49.75° N |
| Longitude | 123.75° W | 124.75° W | 120.25° W |
| Temperature (°C) | | | |
| Annual | +0.7 | +0.8 | +2.5 |
| Dec–Feb | –11.3 | –8.8 | –6.8 |
| Mar–May | +0.9 | +0.4 | +2.0 |
| Jun–Aug | +11.9 | +9.9 | +12.0 |
| Sep–Nov | +1.0 | +1.4 | +2.7 |
| Precipitation (mm day ⁻¹) | | | |
| Annual | 1.7 | 1.6 | 1.6 |
| Dec–Feb | 2.0 | 1.9 | 2.3 |
| Mar–May | 1.2 | 1.1 | 1.4 |
| Jun–Aug | 1.9 | 1.6 | 1.3 |
| Sep–Nov | 1.8 | 1.7 | 1.6 |
| Soil texture | | | |
| | Sandy loam | Loam | Sandy loam |
| Sand (%) | 65 | 42 | 65 |
| Silt (%) | 25 | 40 | 25 |
| Clay (%) | 10 | 18 | 10 |

Table 4. Comparison of IBIS-MIM results for a simulated MPB outbreak with field-, satellite-, and model-based studies (increase: ↑; no change: –; decrease: ↓). Under the “Field”, “Satellite”, and “Model” columns, the numbers refer to the studies listed below. Under the “IBIS-MIM” column, the values in parentheses give the number of grid cells sharing the same qualitative results (only provided when the three grid cells differed).

| Variable | Field | Satellite | Model | IBIS-MIM |
|---|--|-----------------------------------|--|----------------|
| Carbon cycle and vegetation dynamics | | | | |
| Gross primary productivity (GPP) | | ↓ ¹ 1,2 | ↑ ² 13 | ↓ ^a |
| Net primary productivity (NPP) | ↑ ^{3b} 4,5 | | ↑ ^{2,4} 13,5 | ↓ ^a |
| Autotrophic respiration (R_a) | | | ↑ ² 13 | ↓ ^a |
| Heterotrophic respiration (R_h) | | | ↑ ² 13 | ↑ ^c |
| Soil respiration (R_s) | – ^{5,6} | | ↑ ² 13 | ↓ ^a |
| Net ecosystem productivity (NEP) | | | ↑ ² 13 | ↓ ^a |
| Total or aboveground biomass | ↓ ⁵ 6 | | ↑ ^{2,4,6} 13,5,7 | ↓ |
| Dead standing trees | ↑ ⁵ 6 | | ↑ ^{2,6} 13,7 | ↑ |
| Aboveground litter–debris | ↑ ⁷ 8 – ⁵ 6 | | ↑ ^{2,6,8} 13,7,9 | ↑ ^c |
| Total leaf area index (LAI) | ↓ ⁹ 10 | | ↑ ² 13 | ↓ ^a |
| Canopy height | ↓ ⁷ 8 | ↓ ¹ | | ↓ |
| Fractional cover, lower canopy | ↑ ^{10,11} 11,12 – ^{5,8} 6,9 | | | ↑(1) –(2) |
| Grass biomass | ↑ ^{7,8,12} 8,9,13 | | | ↑ |
| Shrub biomass | ↑ ¹² 13 – ^{7,8,9} | | | ↑ (marginal) |
| Energy exchanges | | | | |
| Air temperature (T), summer | ↑ ^{5,10} 16,11 | | | ↑ |
| Land surface T , summer and month prior to snowfall | ↑ ¹⁰ 11 | ↑ ^{11,12} 14 | ↑ ^{14,15} 15,16 | ↑ |
| Soil T , summer | ↑ ^{5,10} 16,11 | | | ↑ |
| ΔT surface vs. air, summer | ↑ ⁷ 10 – ⁸ 11 | | | ↑ |
| Albedo, seasons/annual | | ↓ ^{11,16,17} 11,12,17,18 | | ↑ |
| Latent heat flux, summer | | ↓ ¹³ 14 | ↓ ¹⁵ | ↑(2)d ↓(1)e |
| Sensible heat flux, summer | | ↓ ¹³ 14 | ↓ ^{14,18} 15,19 | –(1)e ↓(2)d |
| Water cycle | | | | |
| Evapotranspiration, summer/annual/n.s. ^f | ↓ ^{19(f)} 20(f) | ↓ ^{11,13} 11,14 | ↓ ^{15,18,19(f)} 16,19,20(f) | ↑(2)d ↓(1)e |
| Transpiration, summer (first two years only) | ↓ ²⁰ 21 | | | ↓ |
| Runoff, annual/n.s. ^g | ↑ ^{19(f)} 20(4) – ^{19(f)} 20(f) | | ↑ ^{15,18,19(f)} 16,19,20(2) | ↑ ^a |
| Peak flow, n.s. ^h | | | ↑ ^{19(f)} 20(2) | ↑ |
| Soil moisture, seasons/annual/n.s. ^f | ↑ ^{5,19(f)} 6,20(f) – ⁵ 6 | | ↑ ¹⁵ 16,18,19,20 – ¹⁶ 19,9 | ↑ ^b |
| Snow depth/amount, monthly/n.s. ⁱ | ↑ ^{19(f)} 21 – ²⁰ 22 – ^{19(f)} 20(2) | | ↑ ^{15,18,19(f)} 16,19,20(f) | ↑ |
| Snowmelt onset, daily/monthly/n.s. ^h | ↑ ^{19(f)} 21 – ²⁰ 22 – ^{19(f)} 20(2) – ^{19(f)} 20(f) | | ↑ ^{15,18,19(f)} 16,19,20(f) | ↓ |

¹ Bright et al. (2013); ² Moore et al. (2013); ³ Edburg et al. (2011); ⁴ Romme et al. (1986); ⁵ Pflefer et al. (2011); ⁶ Morehouse et al. (2008); ⁷ Caldwell et al. (2013);

⁸ Simard et al. (2011); ⁹ Klutsch et al. (2009); ¹⁰ Pugh and Gordon (2013); ¹¹ Griffin et al. (2011); ¹² Vanderhoof et al. (2014); ¹³ Stone and Wolfe (1996);

¹⁴ Maness et al. (2013); ¹⁵ Wiedermyer et al. (2012); ¹⁶ Mikkelson et al. (2013b); ¹⁷ O'Halloran et al. (2012); ¹⁸ Vanderhoof et al. (2013); ¹⁹ “LAI4” case from Chen et al. (2015);

²⁰ 20 studies reviewed in Mikkelson et al. (2013a), the number of different studies being given in italics between parentheses; ²¹ Hubbard et al. (2013); ²² Pugh and Small (2012).

^a Becomes the opposite after ~ 5–15 years in the northern and central grid cells. ^b ↑ after 15–20 years in one out of four cases. ^c Dominant response (high interannual variability). ^d

Except the first year, northern and central grid cells. ^e After 5 years, southern grid cell. ^f The time period for the studies reviewed in Mikkelson et al. (2013a) is not specified (n.s.), so

comparisons with IBIS-MIM results were performed on an annual basis except for peak flow and snow-related variables (performed on a daily basis). ^g Increase in spring and fall,

decrease in summer. ^h For the first ~ 5 years. ⁱ An increase means that snowmelt begins earlier in the year.

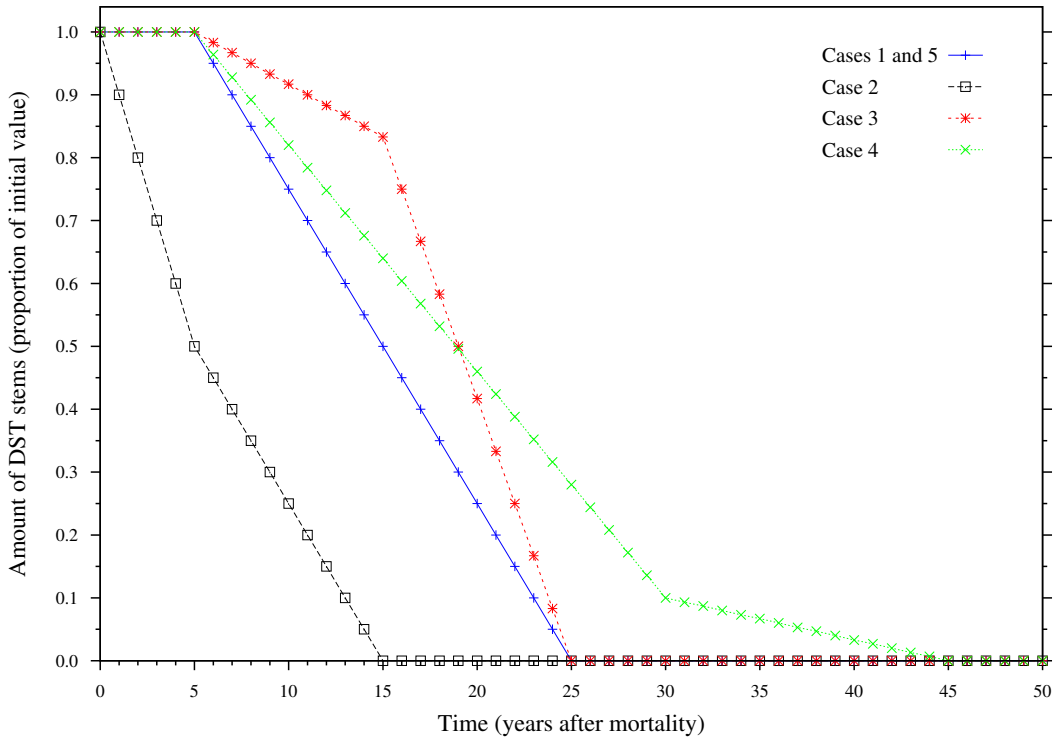


Figure 1. Litterfall schedule of DST stems for the five cases currently implemented in MIM (see Table 2). Mortality happened in year 0 and all values are for the end of the corresponding year.

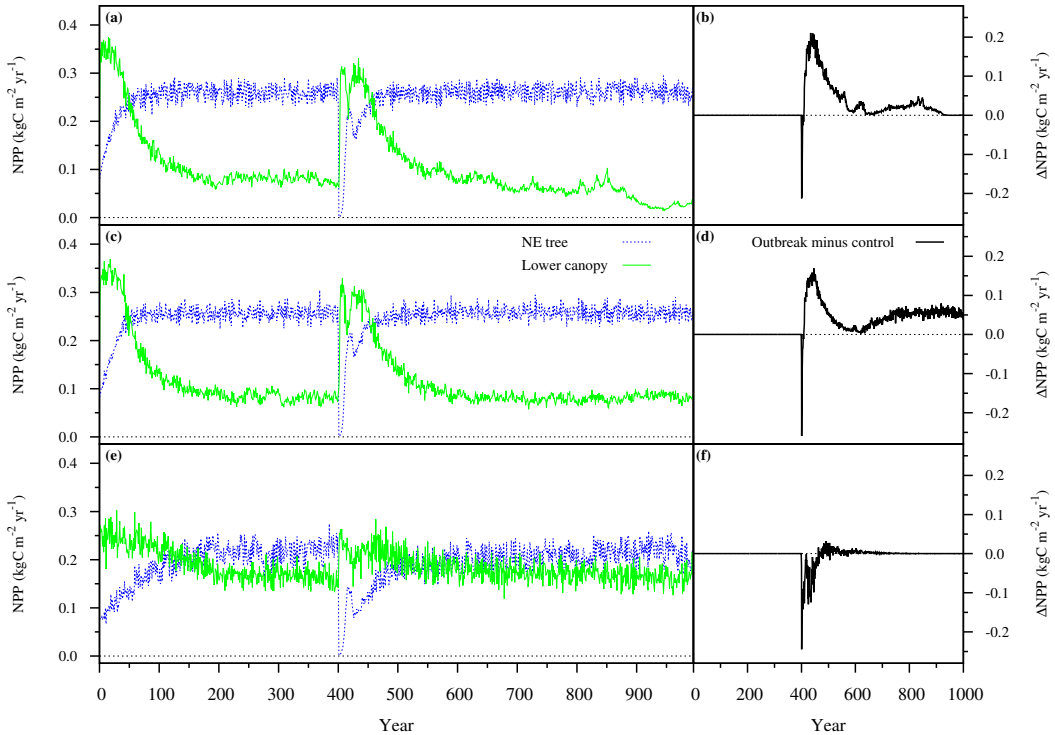


Figure 2. NPP results for an MPB outbreak (100 % mortality on year 401) simulated in IBIS-MIM: NPP of different PFTs (**a**, **c**, and **e**) and difference in total NPP with the control simulation (**b**, **d**, and **f**). NE = needleleaf evergreen; lower canopy = sum of evergreen shrubs, cold-deciduous shrubs, and C_3 grasses. (**a**, **b**) Northern grid cell. (**c**, **d**) Central grid cell. (**e**, **f**) Southern grid cell.

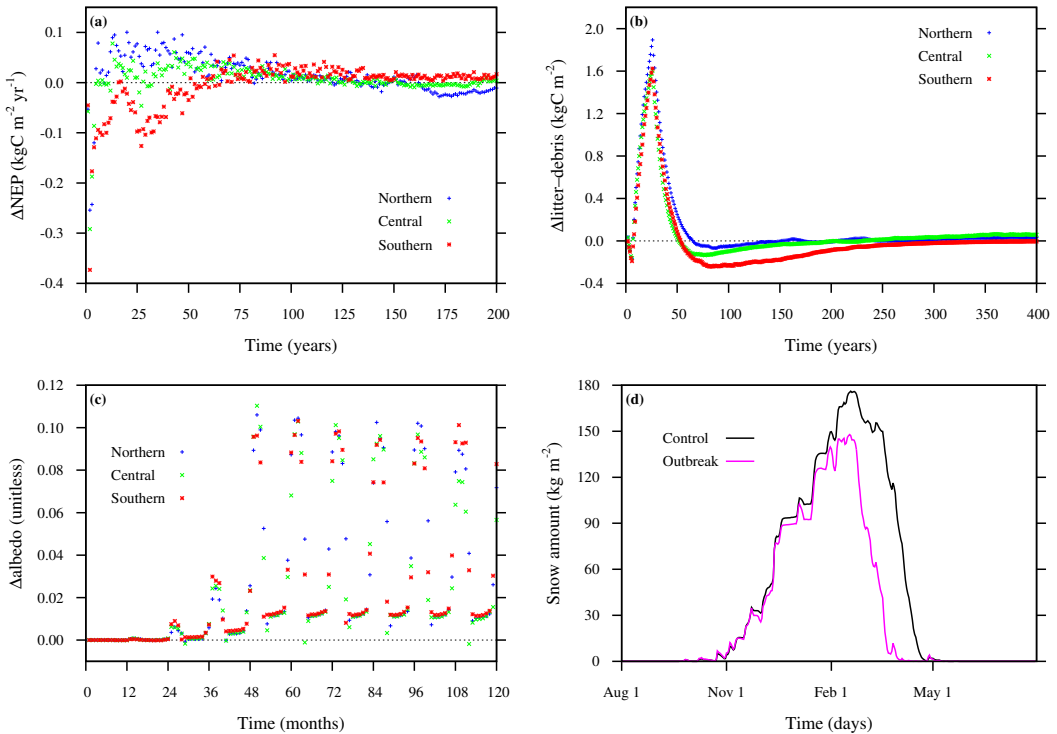


Figure 3. Impact of an MPB outbreak (100 % mortality) simulated in IBIS-MIM on different variables over various timescales. **(a)** Change (outbreak minus control) in NEP for the three grid cells; mortality happened on year 1. **(b)** Change (outbreak minus control) in aboveground litter (including coarse woody debris, but excluding dead standing trees) for the three grid cells; mortality happened on year 1. **(c)** Change (outbreak minus control) in albedo for the three grid cells; mortality happened on months 8 and 9 (August and September). **(d)** Snow amount in the central grid cell for the control and outbreak simulations; mortality happened eight years before.