Elsevier Editorial System(tm) for Cold Regions Science and Technology
Manuscript Draft

Manuscript Number: CRST-D-14-00074R2

Title: Effect of avalanche frequency on forest ecosystem services in a spruce-fir mountain forest

Article Type: Research Paper

Keywords: Carbon; Forest succession; Disturbance; Plant diversity; Rockfall protection; Ungulate habitat

Corresponding Author: Dr. Giorgio Vacchiano, Ph.D.

Corresponding Author's Institution: Università di Torino

First Author: Giorgio Vacchiano, Ph.D.

Order of Authors: Giorgio Vacchiano, Ph.D.; Margherita Maggioni, PhD; Giulia Perseghin; Renzo Motta, PhD

Abstract: Mountain forests provide important ecosystem services, such as protection against natural hazards, carbon sequestration, and plant and animal biodiversity. Natural disturbances occurring in forests can alter the provision of ecosystem services to local and offsite communities, but their influence on multiple service tradeoffs has rarely been analyzed.
Our aim is to analyze the effect of avalanche frequency on the provision of ecosystem services in a mountain forest in the Italian Alps. We sampled tree and understory vegetation, soil carbon, and intensity of the browsing damage at 10 plots at each of the following observation sites: (1) an active avalanche track ("recent disturbance"), (2) an area last disturbed in 1959 by avalanches ("old disturbance"), occupied now by a dense aspen forest, and (3) the regularly managed spruce-fir stand ("control"). We computed metrics of plant diversity (Shannon and evenness indices), aboveground and belowground carbon stocks, and a browsing index on regeneration and shrubs as a proxy for ungulate habitat. Finally, we assessed the ability of forests in each site to mitigate rockfall hazard.
In our study, higher avalanche frequency was associated with lower carbon stock, higher species diversity, and lower protection against rockfall. Of all species found in the avalanche track, 54% were exclusive of that site. After 50 years, the post-disturbance stand provided a very high protection effect against rockfall, but was temporarily unsuitable for wild ungulate habitat, due to the high tree density and lack of open areas. Species richness and diversity were lower in older than in more recently disturbed sites, and not significantly different than the control stand. The control stand fulfilled the requirements for minimal protection against rockfall, but may lose its effectiveness in the near future due to senescence or disturbance-related mortality of canopy trees.
Elucidating the tradeoffs between ecosystem services and disturbance frequency will support managers in planning management actions (e.g., avalanche protection measures), and assess tradeoffs between the need to mitigate risks in the most vulnerable areas and the opportunity to improve the provision of ecosystem services where some disturbance can be allowed to occur.

DISAFA
Università degli studi di Torino
Dipartimento di Scienze Agrarie, Forestali e Alimentari
Via Leonardo Da Vinci, 44 - 10095 Grugliasco (TO)

Science of the Total Environment

Editorial Office

Grugliasco (Italy), 25th March 2014

Dear Editor,

I enclose to the present letter the following manuscript for submission to your journal: "Effect of avalanche frequency on forest ecosystem services in a spruce-fir mountain forest".

The article is original, has not been considered for publication elsewhere in its current version, and has been read and approved by all authors.

The submission consists of this cover letter, the title page, highlights, manuscript text with references and tables, 9 figures in separate files, a KML file, and a supplementary Excel table.

I believe the paper's topic falls neatly into the scope of the journal, since it details the effect of variable time since avalanche disturbance on ecosystem services provided by a mountain forest in the Italian Alps. My co-authors and I would be delighted to have our paper appear in your journal.

I thank you and the reviewers in advance for your efforts in evaluating and critiquing this manuscript. I look forward for your review.

Sincerely,

Giorgio Vacchiano (Corresponding author)

Tel.: +39 011 6705536. Fax: +39 011 6705546.
Email: giorgio.vacchiano@unito.it
Department of Agricultural, Forest and Food Sciences - University of Turin

via L. da Vinci 44, 10095 Grugliasco (TO), Italy

***Response to Reviewers**

General comments:

The quantification of rockfall protection with RockyforNET seems straightforward, but needs some more transparency about parameters entered and comparison between the 3 treatment types. The added expert opinion with NAIS-guidelines is however based on an old and simplified version of these guidelines and should be omitted or strongly improved in a revised version (see also specific comments below)
We removed from the paper all reference (methods, results, discussion, Table 4 and Figure 8) to the analysis based on the old NAIS and kept the quantification by RockforNET, clarifying all parameters used (e.g., rock size, density and shape consistent with bedrock – lines 158-159 and 261-264).

The ecosystem service "habitat for wild ungulates" is based on a browsing intensity index. In my eyes this is not enough and may even be misleading. For example, at least Summer habitats for both Capreolus capreolus and Cervus elaphus are improved with the availability of open areas and herbaceous vegetation (like it is found for example on frequently disturbed avalanche tracks).
Browsing intensity has been used in the past to quantify ungulate habitat (e.g., Moser et al. 2008 For Ecol Manage in windthrow gaps). It is true that browsing on shrubs and tree is indicative of winter foraging by ungulates (which however is the most limiting factor in many instances). We now indicate ungulate habitat by three different metrics: winter habitat (browsing index), summer habitat (percent herb cover), and hiding requirements, following methods by Smith and Long (1987 West J Appl For). See answers to specific comments for details.

I miss a clear synthesis of the 4 addressed ecosystem services and how they are provided in the 3 treatments.
A synthesis has been added at the beginning of the Discussion section (lines 335-342), the Discussions have been clarified with sub-headings pointing to different ecosystem services, and a new Table 5 summarizes the value for different ecosystem services in the three stand.

The research area with the 3 different disturbances treatment seems adequate for the purpose of this study, but some more information on the history (and in particular on the disturbance history) of these treatments would be valuable in order to better evaluate and discuss the results. We know about avalanche events in 1959 and 2009, but what is the expected frequency of such an event? An avalanche dynamic model, cataster data or the available tree ring cores may provide some more information on this.
We prefer not to use a dynamical model but rely on actual avalanche data present in the Cadaster to identify the three different sites. In relation to the disturbance history, besides the description given in the Study area Section, we added more info on the estimated return period of the avalanches for the Recent (R) and Old (O) disturbance plots in their description at line 149 and in Fig. 1, where now more historical avalanches are shown. This helps the reader to know where most of the avalanches flow and the area where the extreme avalanche of 1959 destroyed the forest. After consulting with the Avalanche Service of Aosta Valley, they realized that the outline of the avalanche in their Cadaster was wrong and updated it as now shown in the new Fig. 1.

The control stand seems based on the stand structural attributes to be a young stand with few old trees, so also this stand seems to have an important disturbance and/or management history (see also specific comments below). Generally a clearer description of the site conditions and the disturbance history would contribute to an improved overall discussion of this case study.
The reviewer is right, but we don't have specific information on past management in the control stand. Looking at field evidence (stumps), low CWD amount, and at the reverse-J shape of the diameter distribution, we can assume that this stand was (and still is) treated according to consuetudinary management practices in mixed montane Norway Spruce forests of the Alps, i.e., after recovery from extended clearcuts during Word War II, maintaining an uneven-aged structure by single tree or small group selection every 10-20 years, and promoting groups of naturally established regeneration (Motta et al., 2000, 2010, 2015).

Specific comments:

Line 18: specify (1) a frequently disturbed avalanche track or active avalanche track or recent disturbance (cf line 261 ff), (2) an area last disturbed in 1959 by avalanches or "old disturbance event from 1959 (cf line 261).
Lines 18 and 261 were modified and made consistent

24: higher avalanche frequency was associated with... (in our study)
OK

26: after 50 years, the post disturbance stand provided a very high protection effect against rockfall (can not be generalized, there are certainly examples of other 50-year old post avalanche track with a different development, please specify that protection effect is against rockfall (not against avalanches).
OK

29: may lose instead of will likely lose? (difficult to predict mortality processes in such stands and the long term effect of dead wood against rockfall)
OK

38: the active avalanche track
OK

39: post disturbance stand instead of "forest"
OK

55: In particular "Alpine regions" instead of "for example alpine regions". Almost all related references are from Switzerland.
OK

69: 169 Annex II species?
EDITED: (Annex II of the Habitats Directive 92/43/EEC)

76: term "Alpine forests" : means "forests in the Alps"   if   written with Capital letter. Is this the meaning here? References are more general. -> maybe change to "Many temperate mountain forests are currently carbon sinks.
OK

83: very rare ->   relatively rare
OK

114 ff: can you make clearer that the study area includes 1) the avalanche track, 2) the old avalanche track   and 3) the adjacent forest stand. Useful would be a reference to a figure and numbers, where the 3 different "disturbance treatments" are.
Concerning the history of the plots, we added at line 149-154 : “The latter event had an extraordinary severity, destroying trees in the previously undisturbed forest, and accumulating a deposition height of 20 m in the runout area. From the analysis of historical photos (Fig. 2a) it is evident how the damages to the older forest were produced from the powder component of the avalanche flow; this area is currently occupied by a dense aspen forest (Fig. 2b). At the transition between the track and deposition zones, we identified three different study sites according to the frequency of disturbance, which are shown in Fig. 1 and 2b and described in the next Section.”
At line 166-171 we changed the sentence to include the information on the estimated return period: “We established a chronosequence of increasing disturbance frequency, and decreasing time since last disturbance, by comparing the following sites: 1) recent disturbance (R) by using the track width of the majority of the avalanches recorded in the Cadastre (i.e., avalanche return period of one to few years); 2) old disturbance (O), by reconstructing the perimeter of the 1959 event from pre-disturbance historical aerial imagery (1954) and oblique photographs of the event (i.e., avalanche return period of more than 50 years), and 3) the control (C) forest (regular management no avalanches).”
Furthermore, we added symbols for the three treatments on Fig. 2b.

I would find it useful to have a bit more information on the history of the forest. Is the adjacent (control) stand managed? Are there clear indications that the stand was formerly affected by an even more extreme disturbance event before 1959?
There are no indications of a more extreme avalanche event before 1959. Regarding the history of the control stand, we added the following (line 131-137): “No specific information on past management for the control stand was available. However, looking at field evidence (stumps), low CWD amount, and at the reverse-J shape of the diameter distribution, we can assume that this this stand, owned by the municipality, was (and still is) treated according to consuetudinary management practices in mixed montane Norway Spruce forests of the Alps (at least after World War II), i.e., maintaining an uneven-aged structure by single tree or small group selection

every 10-20 years, and promoting groups of naturally established regeneration (Motta et al., 2000, 2010, 2015)."

140: does "the stand" refer to the" adjacent forest stand next to the avalanche track" or to the whole study area including the avalanche track? Usually, a stand is somewhat more homogenous in terms of forest structure and species composition. Compare also with line 282, where only the active avalanche track is "a stand"
EDITED: the whole study area

155: reference for forest management unit 38?
EDITED: (source: municipal Forest Management Plan)

160: we sampled tree age? -> we estimated tree age based on... or we sampled increment cores for
EDITED: Finally, we estimated tree age based on increment cores extracted at 50 cm height from one randomly selected tree in each of the small (DBH <15 cm), medium (15 <DBH <25 cm), and large (DBH >25 cm) tree size classes per 12m plot.

221: A browsing index is a strong simplification for the habitat requirements of both relevant deer species. This would probably lead to an underestimation of the habitat quality of open avalanche tracks.
We now indicate ungulate habitat by three different metrics: winter habitat (browsing index), summer habitat (percent herb cover), and hiding requirements, following methods by Smith and Long (1987 West J Appl For) based on an empirical relationship between hiding cover and the sum of tree diameters in the stand. Methods, Results, Table 5 and Discussion were modified accordingly (lines 239-257, 317-322, 431-441).

229: I think that the objective quantification of the ecosystem service rockfall with RockforNET (which is also the base for the new rockfall profile in NAIS, see http://www.gebirgswald.ch/de/anforderungen-steinschlag.html) is adequate for such a quantification of ecosystem services and I would focus more on this quantification of rockfall protection instead of describing in detail an old and outdated version of the NAIS rockfall profile.
We removed from the paper all reference (methods, results, discussion, Table 4 and old Figure 8) to the analysis based on the old NAIS and kept the quantification by RockforNET

245: size of stones?
We now simulate protection from two different rock size classes, moderate (50x50x20) and large (100x100x40 cm). Methods, Results, Table 5 and Discussion were modified accordingly (lines 262-263, 323-327, 466).

247 ff: The method for the ecosystem model is not clear for me. Are carbon stock, browsing index and plant diversity index the response variables in the GLM? Why is browsing index (in my eyes not an ecosystem service per se) included and rockfall protection (an ecosystem service) not included in this analysis?
We removed the GLM part from the paper, since it was unnecessary for the quantification of the main 4 ecosystem services provided by the disturbed and nondisturbed forest.

271: I would write "we estimated" when referring to the age of the trees based on your method without cross-dating.
OK

272: The canopy had a variable tree cover of 20-80%
OK

293: The information on soil carbon ratios of different stages of forest development is valuable and not often seen: can you say more about differences in the soil carbon ratios between control, active avalanche track and 1959-disturbance?
Discussion was expanded (lines 352-365).

Also the result that the sum of the species in different post disturbance stages is much higher then species number of just one of these stages is remarkable and could even be stressed more.
Discussion was expanded (line).

304 ff: browsing intensity is a relevant driver for the ecosystem development, and it is certainly interesting to compare browsing intensity in the 3 different (forest) disturbance types, but browsing intensity is not an ecosystem service, so I find it somewhat strange to include it in the same sub-chapter with 2 of the 3 considered ecosystem services. Another option would be to change "browsing intensity" to a more suitable proxy for

"ungulate habitat".
We now indicate ungulate habitat by three different metrics: winter habitat (browsing index), summer habitat (percent herb cover), and hiding requirements, following methods by Smith and Long (1987 West J Appl For) based on an empirical relationship between hiding cover and the sum of tree diameters in the stand. Methods, Results, Table 5 and Discussion were modified accordingly (lines 239-257, 317-322, 431-441).

309 ff: The quantification of the ecosystem service "rockfall protection" is very important for this manuscript. I would focus on the quantitative method with Rockyfor, if possible in combination with an analysis based on the new Rockfall calculation tool of NAIS http://www.gebirgswald.ch/de/anforderungen-steinschlag.html (should actually be in line with your calculation as based on the same method). NAIS is a certainly a very useful practical tool for the management of protection forests (and at least for Switzerland the best available state of the art expert system), but for the purpose of this manuscript I would not emphasis too much on the given qualitative estimations of rockfall protection and on the provided predictions of possible future developments, this for several reasons (….).
We removed from the paper all reference (methods, results, discussion, Table 4 and old Figure 8) to the analysis based on the old NAIS and kept the quantification by RockforNET. Also, considerations about future protective role were removed, to focus on current ecosystem service provision.

322 ff: I don' t really understand this section and would actually expect something like a synthesis of the addressed ecosystem services under the 3 treatments. An analysis of important drivers for these ecosystem services (e.g. in the form of GLMs) can be a part of such a synthesis, but I would expect a clearer declaration of what predictor and response variables are and why. Table 5 provides something like such a table, but I don't understand the selection of the columns (response variables in the GLM, see my comments to the method section of these models)
We removed the GLM part from the paper, since it was unnecessary for the quantification of the main 4 ecosystem services provided by the disturbed and nondisturbed forest. A synthesis of ecosystem service provision now opens the Discussion section (lines 335-342).

337: very high protection agaist rockfall -> high protection against rockfall (for small to moderately sized stones?)
OK

337: The control stand (with more large diameter trees) would probably provide better protection against large stones, but more quantitative analysis are needed to disentangle this.
We now simulate protection from two different rock size classes, moderate (50x50x20) and large (100x100x40 cm). Methods, Results, Table 5 and Discussion were modified accordingly (lines 262-263, 323-327, 466).

431: So if bark beetles is a concern, why is a high percent of spruce on basal area a positive critiera for future rockfall protection (fig. 8)?
These criteria referred to old guidelines and are now removed from the paper.

441 ff: future rockfall protection of the old avalanche track would radically decrease after the next avalanche like the 1959-event. This should be at least discussed here. Generally in order to follow the arguments about future developments of control and old avalanche tracks it would be helpful to add a typical photograph of all 3 disturbance treatment stands. Fig 2b gives an overview, but the control stand is just dark in the shadow.
Considerations about future protective role were removed, to focus on current ecosystem service provision. However, we included 3 images of the three treatments at the beginning of the discussion (new Fig. 8).

Table 1: Was Norway spruce the only conifer? Based on the area description and title, I expect at least fir and also larch. Please provide somewhere a clear description of the dominant species in the 3 disturbance treatments.
Row 1 was set to “Conifers”. Rows for fir and larch composition were added in table 4, consistently with the composition described at lines 281-282, 290, 296-297.

Table 4: I would skip this table or adapt it to a newer version of the rockfall profile of RAMMS (see my comments above).
The table was eliminated.

Table 4 (formerly Table 5): Amount of coarse woody debris is often considered for biodiversity indices (because of the value for animals which are depending on dead wood). Here you focus on plants, but maybe you

could at least add a sentence in the discussion about the option of including dead wood as proxy for habitats or biodiversity.
ADDED (lines 423-428)

Table 4 (formerly Table 5): Again no other conifers then spruce? What about fir (cf. Title of the manuscript and Fig. 5)
Fir and larch were added to Table 4.

Table 4 (formerly Table 5): Herb cover is obviously much higher in the recent disturbance. This is a very relevant proxy for habitats of Cervus and Capreolus and should be included in the formula of this proxy.
We now indicate ungulate habitat by three different metrics: winter habitat (browsing index), summer habitat (percent herb cover), and hiding requirements.

Table 4 (formerly Table 5): Regeneration density (what is included here? Please provide size thresholds).
Regeneration threshold is H >10 cm, DBH <2.5 cm, as was indicated in Methods (line 180) and now also in the Table footnote.

Depending on such size thresholds the regeneration density in the control seems very high (both for spruce and broadleaves), so it seems not obvious that the future of the protection against rockfall in this control stand may be endangered.
Considerations about future protective role were removed, to focus on current ecosystem service provision.

Table 6: It is difficult to understand the selection of these variables: 2 proxy for diversity, 2 proxy for Carbon, no proxy for rockfall. Instead one proxy for browsing intensity (which is in my eyes not an ideal habitat proxy, because deers show also preferences for open areas with herbaceous vegetation. So the habitat quality of the active avalanche track may be underestimated if only considering browsing intensity.
As detailed above, ungulate habitat now has three proxies. The GLM part was removed from the paper.

Fig. 1: What means "avalanche perimeter"? Is this based on an avalanche model or based on an avalanche cataster? Obviously the 1959 event was outside of the avalanche zone! A simulation with an avalanche dynamic model or cataster data may help.
As outlined in the answers to General comments told before, we changed the Figure to include more information, coming from the Avalanche Cadastre, not from an avalanche dynamic model.
New caption: "Study area location, maximum avalanche perimeter from the regional avalanche cadaster (CRV) and sampling design. Colored perimeters represent several occurrences of the avalanche as recorded by CRV. White dots: recent avalanche site; grey dots: old avalanche site; black dots: control site."

Fig. 3: Some figures are surprising: for example it seems that %spruce is much lower in the control plots then in the old avalanche. In contrast % broadleaved trees is higher in the control. This contradicts to table 4 and to what one could expect based on Fig2b and the text.
EDITED: Figures in Fig. 3 have been corrected.

Fig. 3: What is the definition for seedlings here?
EDITED: regeneration (consistent with Methods, line 180 and Table 4).

Fig. 4: The dhh and age distribution of the control plot indicate that this is a also a very young stand with some older trees. So based on these information, it looks like this is also something like a post-disturbance stand with some remnant older trees. Is it possible that most trees of the control stands were also affected by the 1959 avalanche (pressure of powder cloud if it was pa powder avalanche)? Or was it formerly an open grazed or formerly heavily managed forest? More information on the disturbance history of the control would be useful and depending on this history it would be necessary to change the term "undisturbed control" in line 107.
The reviewer is right, the stand was likely regularly managed. We added information on management at lines 131-137 and changed "undisturbed" to "regularly managed" throughout the paper.

Fig. 5: Is this over all 3 treatments?
Yes. ADDED: "All treatments pooled"

Fig. 8: I would skip this figure or at least adapt it to a newer version of NAIS, see my comments above
The figure was eliminated.

***Highlights (for review)**

- ● We quantified ecosystem services in a spruce-fir forest under variable avalanche frequency.
- ● The avalanche track had higher plant diversity and lower carbon (C) stocks.
- ● 50 years after disturbance, the forest was dominated by aspen, and optimal for rockfall protection.
- ● Wild ungulates found suitable habitats in the avalanche track and in the control.
- ● Maintaining avalanche-disturbed areas in the landscape can benefit biodiversity and wildlife habitat.

Effect of avalanche frequency on forest ecosystem services in a spruce-fir mountain forest

Giorgio Vacchiano* [a,b], Margherita Maggioni[a,b], Giulia Perseghin[a], Renzo Motta[a,b]

a. Department of Agricultural, Forest and Food Sciences, Università di Torino, Largo Braccini 2, 10095 Grugliasco (TO) – Italy.

b. NatRisk - Centro interdipartimentale sui rischi naturali in ambiente montano e collinare, Università di Torino, Via Leonardo da Vinci 44, 10095 Grugliasco (TO) – Italy.

* Corresponding author. tel +39 (0)11 6705536, fax +39 (0)11 6705536. Email giorgio.vacchiano@unito.it

Other author emails: margherita.maggioni@unito.it, renzo.motta@unito.it

Abstract

Mountain forests provide important ecosystem services, such as protection against natural hazards, carbon sequestration, and plant and animal biodiversity. Natural disturbances occurring in forests can alter the provision of ecosystem services to local and offsite communities, but their influence on multiple service tradeoffs has rarely been analyzed.

Our aim is to analyze the effect of avalanche frequency on the provision of ecosystem services in a mountain forest in the Italian Alps. We sampled tree and understory vegetation, soil carbon, and intensity of the browsing damage at 10 plots at each of the following observation sites: (1) an active avalanche track (“recent disturbance”), (2) an area last disturbed in 1959 by avalanches ("old disturbance”), occupied now by a dense aspen forest, and (3) the regularly managed spruce-fir stand (“control”). We computed metrics of plant diversity (Shannon and evenness indices), aboveground and belowground carbon stocks, and a browsing index on regeneration and shrubs as a proxy for ungulate habitat. Finally, we assessed the ability of forests in each site to mitigate rockfall hazard.

In our study, higher avalanche frequency was associated with lower carbon stock, higher species diversity, and lower protection against rockfall. Of all species found in the avalanche track, 54% were exclusive of that site. After 50 years, the post-disturbance stand provided a very high protection effect against rockfall, but was temporarily unsuitable for wild ungulate habitat, due to the high tree density and lack of open areas. Species richness and diversity were lower in older than in more recently disturbed sites, and not significantly different than the control stand. The control stand fulfilled the requirements for minimal protection against rockfall, but may lose its effectiveness in the near future due to senescence or disturbance-related mortality of canopy trees.

Elucidating the tradeoffs between ecosystem services and disturbance frequency will support managers in planning management actions (e.g., avalanche protection measures), and assess tradeoffs between the need to

mitigate risks in the most vulnerable areas and the opportunity to improve the provision of ecosystem services where some disturbance can be allowed to occur.

Highlights

- We quantified ecosystem services in a spruce-fir forest under variable avalanche frequency.
- The active avalanche track had higher plant diversity and lower carbon (C) stocks.
- 50 years after disturbance, the post-disturbance stand was dominated by aspen, and optimal for rockfall protection.
- Wild ungulates found suitable habitats in the avalanche track and in the control.
- Maintaining avalanche-disturbed areas in the landscape can benefit biodiversity and wildlife habitat.

Keywords

Carbon; Forest succession; Disturbance; Plant diversity; Rockfall protection; Ungulate habitat

Introduction

Mountain forests throughout the world provide a variety of important ecosystem services, including protection against natural hazards (e.g., floods, avalanches, and landslides), carbon sequestration, provision of natural resources (e.g., dairy products, timber as renewable raw material for energy production and for construction), tourism and recreation, fresh water regulation, and plant and animal biodiversity (Gret-Regamey et al., 2008a). Even where production or supply services are not the main interest, e.g., in those parts of the Alps where timber extraction has ceased to be profitable due to socio-economic changes (Walther, 1986; Conti and Fagarazzi, 2004), regulatory functions play an important role for both local and offsite communities.

In particular, Alpine regions have developed programs to identify and manage direct protection forests, i.e., forests that protect human settlements or infrastructures from gravitational hazards such as rockfall, avalanches, and debris flow (Brang, 2001; Berger and Rey, 2004; Brang et al., 2006; Wehrli et al., 2007). The effectiveness of forest stands, or of specific stand structures, in mitigating natural hazards has been assessed by field surveys, experiments, and empirical or physical models (Motta and Haudemand, 2000; Dorren et al., 2004; Bigot et al., 2008; Teich et al., 2013). Such research has provided land administrators with quantitative tools to assess risk and management priorities in time and space (Frehner et al., 2005, Gret-Regamey et al., 2008b; Teich and Bebi, 2009; Olschewski et al., 2012), and has enabled science-based allocation of resources to maintain, promote, or rehabilitate the forest protective function.

From the biodiversity point of view, the Alps exhibit a complex geomorphology and an array of microclimates which contribute to a wide variety of habitats (i.e., 100 of 198 habitat types listed in Annex I of the Habitats Directive 92/43/EEC), and high levels of biodiversity. The alpine biogeographic region of Europe hosts about 7000 plant species (Ozenda and Borel, 1994), that is more than a third of the flora recorded in Europe west of Urals, and almost 400 endemic plants (Aeschimann et al., 2012). The fauna of the Alps might reach 30,000 species (Chemini and Rizzoli, 2003). A total of 165 species and subspecies are highly protected (Annex II of the Habitats Directive 92/43/EEC), while the region includes important refugia for plants and especially for animals with large home range requirements (Condé et al., 2006). In the 20th century, the abandonment of mountain fields, meadows and grazing lands, and the expansion of shrubs and forests with an accompanying reduction of clearings, as well as the intensification of tourism and human presence, have greatly affected suitable habitats for plant and animal species, determining an increase of forest-related taxa and a demise of grassland species (Laiolo et al., 2004; Falcucci et al., 2006; Niedrist et al., 2008; Pellissier et al., 2013).

Finally, many temperate mountain forests are currently a carbon sink (Goodale et al., 2002; Ciais et al., 2008), due to their predominantly young age, the naturally occurring afforestation of fallow lands, and the ongoing environmental changes, i.e., climate warming and nitrogen (N) deposition (Bellassen et al., 2011). However, adapting forest management to maximize carbon stocking is subject to many uncertainties, such as the quantity and processes of carbon in the forest soil (Lal, 2005), or the effect of natural disturbances (Gimmi et al., 2008; Liu et al., 2011).

Disturbances are ubiquitous in forest ecosystems (Franklin et al., 2002). In forests of the European Alps, large, stand-replacing disturbances are relatively rare due to the high degree of landscape fragmentation and to the pervasive control by man, e.g., by active fire and avalanche suppression (Kulakowski et al., 2006; Brotons et al., 2013) or insect outbreak monitoring and control (Faccoli and Stergulc, 2004). However, disturbances still occur at spatio-temporal scales relevant to the provision of ecosystem services to local communities, e.g., in occasion of extreme fire seasons (Veraverbeke et al., 2010), regional drought spells inducing forest decline events (Rigling et al., 2013), or extra-tropical cyclones (Ulbrich et al., 2001). Recent research has been addressing the questions related to: a) the quantification of ecosystem services (Millennium Ecosystem Assessment, 2005; Haines-Young et al., 2012), b) the resolution of conflicts between non-compatible ecosystem services (Nelson et al., 2009; Bullock et al., 2011; Briner et al., 2013; Gret-Regamey et al., 2013), and c) the impact of climate change on the provided services (Metzger et al., 2006; Lindner et al., 2010; Elkin et al., 2013). However, the influence of natural disturbances on multiple service tradeoffs has rarely been analyzed (e.g., Spencer and Harvey, 2012), especially in forest ecosystems.

Avalanches are one of the dominant disturbance agents in the Alps (Bebi et al., 2009). High-frequency avalanches shape the ecosystem in which they occur, and exert a strong selective pressure on plant and animal species living in the avalanche track and runout zone (Butler, 1985; Rixen et al., 2007). On the other hand, low-frequency, high-intensity events have the potential to reset the ecological succession, by replacing mid-seral species by early-seral colonizers capable of taking advantage of the new environmental conditions in the avalanche aftermath (Erschbamer, 1989). In both cases, avalanches can greatly affect the provision of ecosystem services and the functioning of forest ecosystems, not only in the area directly perturbed (Viglietti et al., 2010), but also at landscape scale, e.g., by modifying connectivity and the spatial pattern of the forest matrix (Butler, 2001). However, their role in relation to the provision of ecosystem services is still unexplored.

The aim of this paper is to analyze the effect of avalanche frequency on the provision of ecosystem services in a mountain forest. We quantified carbon stocking, wild ungulates habitat, plant diversity, and rockfall protection and compared all of them across three contiguous sites of (1) a yearly disturbed area, (2) a 50-years old disturbance, and (3) an regularly managed forest not disturbed by avalanches ("control"). Finally, we modeled the effect of disturbance frequency and other environmental predictors (i.e., stand structure, species composition, and soil cover classes) on the current level of forest ecosystem service provision, in order to assess which agent was responsible of the largest effects on the chosen services.

Area description

Our study area (Fig. 1) is the Cranmont avalanche path, in the municipality of Pré Saint-Didier (Aosta, Italy: 45°45'54" N, 6°59 '12" E). The avalanche track runs in the gully of the Crammont creek from 2680 to 1030 m a.s.l. on a northeast-facing slope. The mean slope angle of the release zone is 35°. Mean annual temperature and precipitation at the runout zone are 6.9 °C and 1072 mm, respectively (interpolation of observed data for the years 1950-2000) (Hijmans et al., 2005). Below the timberline (at 2000-2250 m a.s.l.), forests are dominated by European larch (*Larix decidua* Mill.) in the subalpine belt (Habitat 9420 of the Directive 91/244/CEE) and Norway spruce (*Picea abies* (L.) Karst.) in the montane belt (Habitat 9410), with sporadic Scots pine (*Pinus sylvestris* L.) on rock ridges, silver fir (*Abies alba* Mill.) at locally moister sites, and broadleaves such as aspen (*Populus tremula* L.), birch (*Betula pendula* L.), and willow (*Salix caprea* L.). According to a recent regional forest inventory (Camerano et al., 2007), stand density, quadratic mean diameter, and dominant height in the area are in the range of 160-680 trees ha^{-1}, 23-35 cm, and 15-26 m, respectively.

No specific information on past forest management in the study area was available. However, looking at field evidence (stumps), low deadwood amount, and at the reverse-J shape of the diameter distribution (see below), we can assume that this stand was (and still is) treated according to consuetudinary management practices in mixed montane Norway Spruce forests of the Alps, i.e., after recovery from extended clearcuts during Word War II, maintaining an uneven-aged structure by single tree or small group selection every 10-20 years, and promoting groups of naturally established regeneration (Motta et al., 2000, 2010, 2015).

The Regional Avalanche Cadastre (CRV) (Lunardi et al., 2009) reports that the avalanche occurred 72 times between 1913 and 2011, preferably in January or February (35 occurrences), and was characterized by a variable behavior and severity. The avalanche type has been either loose snow or slab (width of starting zone: few to 300 m). The avalanche has repeatedly damaged human infrastructure in the runout zone (two records of housing damage, eight records of road damage). Information from the local people implied that the avalanche usually occurs, not necessarily in its largest potential extent, many times a year (up to ten times depending on the snow conditions). In a winter season, the first events often run straight down to the Dora Baltea river, while the latter ones, influenced by the previous deposits, tend to be deflected towards the North (Fig. 1). In case of large events in the advanced snow season, the avalanche can more easily have a larger width and overcome its yearly track to the South, influencing the older forest. Damage to the forest outside the common avalanche track has been recorded on December 24th, 2009, and December 29th, 1959 (Fig. 2a). The latter event had an extraordinary severity, destroying trees in the previously undisturbed forest, and accumulating a deposition height of 20 m in the runout area. From the analysis of historical photographs (Fig. 2a) it is evident how the damages to the older forest were produced from the powder component of the avalanche flow; this area is currently occupied by a dense aspen forest (Fig. 2b). At the transition between the track and deposition zones, we identified three different study sites according to the frequency of disturbance (Fig.1, Fig. 2b), which are described in the next Section.

Finally, the whole study area is mapped as a direct protection forest, (Meloni et al., 2006), i.e., one that protects downslope human settlements and infrastructures from gravitational hazards. Here, the hazard is represented by rockfall potentially released from within-forest cliffs at elevations of about 1500-1700 m a.s.l. The bedrock in Cranmont is made of metamorphic units belonging to the North-Pennidic domain of the Alps (Sion-Courmayeur Zone), with alternating calcite marble and micaceous-chloritic carbonates schists (Perello et al. 1999). The width of the rockfall-source area is about 300 m, but there is considerable potential for lateral rockfall spread due to the fan-shaped topography of the slope. Individual rocks witnessed in the field ranged from 10 to 100 cm in average diameter.

Material and methods

Sampling design

We established a chronosequence of increasing disturbance frequency, and decreasing time since last disturbance, by comparing the following sites: 1) recent disturbance (R) by using the track width of the majority of the avalanches recorded in the Cadastre (i.e., avalanche return period of one to few years); 2) old disturbance (O), by reconstructing the perimeter of the 1959 event from pre-disturbance historical aerial imagery (1954) and oblique photographs of the event (i.e., avalanche return period of more than 50 years), and 3) the control (C) forest (regular forest management, no avalanches). In order to control for undesired topographic and climatic variability, we constrained sampling between elevations of 1125 and 1300 m a.s.l., corresponding to the top and bottom boundary of forest management unit 38 (source: municipal Forest Management Plan). Within each site, we randomly established 10 sampling plots, ensuring a minimum distance of 20 m from the site edge, and of 25 m between plots. The maximum distance between any two plots was 280 m (Fig. 1).

Sampling was carried out in summer 2012. In each plot we sampled the following: (1) diameter at breast height (DBH), height (H) and species of all living trees (DBH >2.5 cm) within a 12 m radius from the plot center; (2) percent cover by the tree, shrub, herbaceous layers, and exposed mineral soil, within a 5 m radius from the plot center; (3) species and frequency of all regeneration individuals (H >10 cm, DBH <2.5 cm) in the 5 m plot; (4) species and visually estimated cover of each vascular plant in the 5 m plot (floristic nomenclature according to Aeschimann et al., 2004); (5) severity of browsing damage (0:none, 6: 100% browsing or dead individual) (Motta, 1996) to all regeneration individuals and shrubs within each 5 m plot. Finally, we estimated tree age based on increment cores extracted at 50 cm height from one randomly selected tree in each of the small (DBH <15 cm), medium (15 <DBH <25 cm), and large (DBH >25 cm) tree size classes per 12m plot.

For the analysis of carbon stocks, we sampled the following: (6) height and average crown radius (CR) of all shrubs with CR >100 cm; (7) diameter and decay class (1: sound, 3: soft) of all coarse woody debris (CWD) elements (diameter > 10 cm) along two perpendicular linear transects (length =24 m per transect) concentric to the plot center; (8) herbs and litter in three 40x40 cm subplots, at the plot center and at a 2 m distance in a northward and southward direction; (9) mineral soil at 0-5 cm depth, sampled at each subplot by using a 5 cm x 25 cm^2 metal cylinder. Herbs, litter, and soil samples were subsequently pooled, oven dried (105 °C for 72 hours) and weighted in the lab to obtain their biomass; soil samples were preliminarily sieved at 0.5 mm.

Data analysis

For each sampling plot, we computed total tree density, basal area, species composition by density and basal area, quadratic mean diameter (QMD), mean height, and total tree volume (V) by applying DBH-to-volume equations for spruce (Nosenzo, 2005) and broadleaves (Castellani et al., 1984). Following preparation of tree cores (Stokes and Smiley, 1996), we computed the total tree age at coring height from each core by summing the tree ring count and an estimate of missing rings near the pith obtained by means of a pith locator. Using the sample of measured ages, we fitted a linear Age-DBH model for each, and used it to compute missing ages for all tallied trees.

The volume and dry biomass of coarse woody debris (W_{CWD}) were obtained by applying the equations for line intercept sampling (Pearson et al., 2007) (Equation 1):

[1] $$W_{CWD} = -\frac{1}{8}\rho L \sum \left(d_{CWD}^{2} k\right),$$

where L is transect length, d_{CWD} is the measured diameter of each coarse woody debris element, and k is the wood density associated to each decay class (class 1: 0.43 t m^{-3}, class 2: 0.34 t m^{-3}, class 3: 0.19 t m^{-3}) (Pearson et al., 2007). The dry biomass of living trees (W_T) was obtained by applying a biomass expansion equation to the total standing volume of each plot (Penman et al., 2003) (Equation 2):

[2] $$W_T = (1 + R)(V \times BEF \times k_T),$$

where BEF is biomass expansion factor, R is the belowground:aboveground biomass ratio, and k_T is species-specific wood density (Table 1). Shrub biomass (W_S) was computed allometrically (Ohmann et al., 1976) (Equation 3):

[3] $$W_S = ax^b,$$

where x is shrub height for hazel (*Corylus avellana* L.) and crown area (CR^2) for all other species, and a and b are species-specific allometric coefficients (Table 2). Carbon in the coarse woody debris, trees, shrubs, herbs, and litter fractions was computed on a per-hectare basis by assuming a carbon content of 50% in the dry biomass. Soil carbon content ($C_{\%}$) was determined in the lab by dry combustion using a Carlo Erba elemental analyzer, and subsequently converted to carbon biomass on a per-hectare basis (C_{soil}) (Equation 4):

[4] $$C_{soil} = C_{\%} \times BD \times depth,$$

where BD is dry bulk density of the soil, and depth is the sampled soil depth (5 cm).

Plant diversity was assessed at the plot level by computing total species richness (SR), Shannon diversity index (H', Equation 5) and Shannon equitability index (E, Equation 6) (Magurran, 1988):

[5] $$H' = -\sum p_i \ln p_i$$

[6] $$E = \frac{H'}{\ln SR},$$

where p_i is the relative abundance of species *i* in the plot. Species marked as sporadic were assigned an abundance of 0.3 (Reichelt and Williams, 1973).

Ungulate habitat (red deer *Cervus elaphus* and roe deer *Capreolus capreolus*) was assessed by three different indices, taking into account seasonal food availability and hiding cover requirements (Black et al., 1976). Summer food availability was quantified using the sum of herbaceous and shrub cover as a proxy (Moser et al., 2008). Winter food availability, critically important to both red and roe deer, was assessed by computing a browsing index (IB) on shrubs and regeneration for each plot (Boulanger et al., 2009) (Equation 7):

[7] $$IB = \sum \frac{p_i dam_i}{p_i pal_i},$$

where dam_i and pal_i are the average browsing damage and palatability (Table 3) of species i, respectively. Browsing intensity has been used in the past to assess habitat use by wild ungulates (Moser et al., 2008), and can be indicative of winter use if computed on resources normally grazed during such season, i.e., in the absence of herb cover. Finally, deer hiding cover (HC) was estimated as a function of the sum of tree dbh in a stand (Equation 8), using a trigonometric algorithm previously developed for lodgepole pine (*Pinus contorta* Douglas) (Smith and Long, 1987). The algorithm assumes uniform tree spacing and crown height higher than 1 m (i.e., tree crowns do not contribute to hiding), and assumes that hiding cover is adequate when an average of 90% of an adult elk is hidden at a distance of 60 m.

[8] $$HC = 100 - 115.8(0.61)^{0.0003937 \sum dbh}$$

Finally, we assessed rockfall protection by using the online tool RockforNET, that computes the percentage of rocks that surpasses the forested area (Probable Residual Rockfall Hazard, PRH) given rock size, topography, and stand structural characteristics (Berger and Dorren, 2007). Parameters entered in RockforNET were: rock density = 2700 km m^{-3}, rock shape = rectangle, rock dimensions = (a) 50x50x20 cm (moderate size) and (b) 100x100x40 cm (large), height of cliff = 50 m, mean gradient of the slope = 35°, length of unforested slope = 20 m. The length of forested slope was set at a constant value of 250 m in order to make meaningful comparisons between stands regardless of their actual position on the slope (Cordonnier et al., 2013). Stand density, basal area (dbh > 8 cm), and tree species composition were entered on a per-plot basis.

Carbon stock, ungulate habitat metrics, plant diversity metrics and PRH were compared across sites by means of non-parametric Kruskal-Wallis test with pairwise post-hoc Tukey comparison ($p < 0.05$).

Results

Forest and vegetation structure

The avalanche radically changed the forest composition and structure (Table 4) in both the avalanche recent disturbance and the old disturbance. The main impacts of increasing avalanche frequency were: lower tree age and size, higher share of deciduous species in both adult and juvenile layers, higher shrub and herb cover, and a bell-shaped response of tree density and cover (i.e., higher for intermediate time since disturbance) (Fig. 3). Between-plot variability was generally higher in the old disturbance and control sites, while the recent disturbance site exhibited pretty homogenous conditions, except for herb, shrub, and bare soil cover.

In the control area the forest was dominated by Norway spruce (53% basal area on average), silver fir (20%), and larch (10%), with sporadic broadleaves (0-20%). The trees were quite dense (1760 per hectare on average, DBH >2.5 cm), with a mean diameter around 21 cm and a typical uneven-aged size distribution (Fig. 4). Maximum tree age in the dendrochronological subsample trees ranged from 71 years (aspen) to 210 years (spruce); after fitting DBH-age models (Fig. 5), we estimated that the oldest trees in the control area could be around 230 years old. The canopy had a variable tree cover of 20-80%, with treefall gaps allowing the accumulation of coarse woody debris on the ground, and the establishment of dense patches of regeneration of spruce and broadleaves alike. Herb and shrub cover were scarce (5% and 13% on average, respectively).

In the old disturbance site the forest was dominated by a dense layer of pole-stage aspen (4000 trees per hectare on average, QMD = 13 cm) (Table 4). The canopy was closed. Spruce was less abundant both in the canopy (37% of basal area on average) and in the regeneration layer, except for some older spruce trees (>100 years) that were probably left as living legacies from before the last disturbance event. Mean tree age (from both measured and modeled ages) was 45 years; some spruce trees older than 50 years were found, probably as legacies of the pre-disturbance stand (i.e., trees that were tilted but not broken by the avalanche), but none was older than 130 years (Fig. 6).

Finally, in the avalanche track, the high frequency of disturbances resulted in a young stand dominated by young, sprouting broadleaves (98% of basal area on average, QMD = 6 cm). All trees were younger than 50 years (mean tree age: 24 years), and most stems were shorter than 8 m in height. Tree density, volume, basal area, and tree cover were all very low (Table 4). Regeneration was dominated by deciduous species, reaching up to 375.000 per hectare when individual sprouts on each stump were counted.

Ecosystem service assessment

The average amount of carbon in the aboveground, belowground, coarse woody debris, litter, and soil compartments was inversely proportional to the disturbance frequency, i.e., higher in the control and lower in the avalanche track (Fig. 7). The latter had more carbon in the herb and shrub layers, but the total amount was significantly higher in the control stand (400 Mg ha^{-1} on average) (Table 5). Soil carbon usually accounted for about 50% of the total. C/N ratio varied in the range of 18-26 in the control, 17-25 in the old disturbance, and 17-22 in the recent disturbance site.

Species richness of the regeneration, shrub and herbaceous layers in the control, old avalanche, and recent avalanche was 44, 43, and 77 species, respectively (Supplementary material S1). Out of 98 species found, 27 were common to all sites, while 42 were exclusive of the avalanche track (i.e., 54% of all species found in that site). Six species were exclusive of the old disturbance, and only eleven of the control. Consequently, the avalanche track showed the highest plant diversity (Shannon index), although evenness was lower than in the other two sites, due to the dominance of a few shrubs (hazel: 32% average cover, *Salix purpurea*: 6%, *Lonicera nigra*: 6%), and graminoid species (especially *Trisetum flavescen*s, 9%). The old disturbance and control did not differ significantly in their diversity indices (Table 5).

Winter resource use by ungulates (i.e., intensity of browsing on regeneration and shrubs) was highest in the control plots and lowest in the old disturbance ($p < 0.05$), even if with a very large variability throughout the study area (0 to 90%). Silver fir was the most damaged species, followed by hazel, *Lonicera* (among shrubs), aspen, *Salix*, and *Acer* (among tree species) (Table 3). Summer resource availability (herb and shrub cover) and hiding cover by trees were respectively higher and lower in the recent disturbance site (Table 5).

The most effective stand for rockfall protection was the old disturbance site. Currently, PRH against moderate-sized rocks reaches 95% in both the old disturbance and the control sites, and decreases to 83 and 74% respectively on large-sized rocks. In the avalanche track the protection effect is negligible (mean PRH: 11% against moderate sized rocks, and 4% against large rocks), due to insufficient tree density and large treeless areas (Table 5).

Discussion

Following stand-replacing disturbance, the dominant spruce-fir canopy (Fig. 8c) is replaced by early-seral broadleaves (Fig. 8a), eventually dominated by aspen that forms a dense pole-stage forest 50 years after the event (Fig. 8b). Spruce and fir regeneration can then establish below the aspen layer, taking advantage of its higher shade tolerance, of seeds dispersed by trees surviving the avalanche, and of disturbance legacies such as coarse woody debris and pit-mound topography (Bottero et al., 2013).

In the study area, higher avalanche frequency was associated with: (1) lower aboveground and belowground carbon stock, (2) higher species richness (but no change in diversity), (3) higher summer resource availability, intermediate winter resource use and lower hiding cover for wild ungulates, and (4) lower protection against multiple-sized rockfall. After 50 years, high stem density of post-disturbance stands was optimal for protection against rockfall and ungulate hiding requirements, but at the same time resulted in poor resource availability for wild ungulates due to the scarce herb and regeneration cover. Species richness and diversity in the old disturbance site were not significantly different than the control, where the forest was managed according to common single tree selection silvicultural practices.

Carbon stock

Carbon stocks followed a predictable gradient of post-disturbance recovery and buildup. Many studies of carbon stocks in post-disturbance chronosequences have highlighted a carbon source/sink dynamics for stand-replacing disturbance, involving a rapid pulse emission followed by net uptake that gradually declines with the ageing of the canopy (Richter et al., 1999; Thornton et al., 2002; Bond-Lamberty et al., 2004; Pregitzer and Euskirchen, 2004; Gough et al., 2007). In our study area, the regularly managed forest stocked about 400 Mg C ha^{-1} on average. Values for aboveground carbon stocks were consistent with those found in undisturbed spruce forests of the Alps (e.g., 207 Mg C ha^{-1} in living trees at 130 years of age, Thuille et al., 2000). Soil stocks (>200 Mg C ha^{-1} on average) were higher than some values found in literature for comparable ecosystems (e.g., 81 to 188 Mg C ha^{-1} in the organic and mineral layers on acidic soils in Austria: Berger et al., 2002; Pötzelsberger and Hasenauer, 2015) but consistent with uneven-aged spruce forests of similar age in boreal ecosystems (e.g., 199 Mg ha^{-1}: Nilsen and Strand, 2013). Unless significantly disturbed by stochastic agents (e.g., wind damage, bark beetles, exceptional avalanches), the spruce forest has the ability to function as a sink well into its maturity stage, as shown by recent research on managed and old-growth forest (Zhou et al. 2006; Luyssaert et al. 2008; Gleixner et al. 2009; Krug et al. 2012). The effect of different types of forest management on soil and total C sink, however, is still uncertain, but greatly depends on the intensity and frequency of tree removals (e.g., Jandl et al., 2007; Nave et al., 2010; Nilsen and Strand, 2013). The fact that soil is stocking more than 50% of overall ecosystem C is well acknowledged by the literature (Lal, 2005) but rarely measured in the field and often overlooked when computing sequestration/emission balances in forest ecosystems. The belowground : aboveground C ratio did not differ between the old disturbance site and the regularly managed forest, suggesting the absence of significant species-specific differences in root turnover and carbon mineralization rate.

The 50-years old aspen forest is stocking about 200 Mg C ha^{-1} on average, corresponding to a mean uptake of about 3 Mg C ha^{-1} per year (assuming a baseline similar to the C stocked in the recently disturbed site following the last avalanche event). The maximum net biomass production for aspen is reported to occur after 18–32 years (Rytter and Stener, 2005). This reflects the very active juvenile growth during which the volume production per unit area of early-seral species such as aspen may exceed that of Norway spruce (*Picea abies*) (Børset, 1960). Starting at about 60 years of age, however, aspen stands gradually reach a state of decline when mortality exceeds growth (Pothier et al., 2004). Therefore, when averaged over the entire life cycle, the more shade-tolerant Norway spruce allows for higher density and volume at similar site productivity indices (Børset, 1960). Light demanding aspen and shade-tolerant spruce may supplement each other, if they constitute separate overstorey and understorey, respectively (Langhammer, 1982). However, the stand will gradually develop along a successional process leading to dominance of the spruce-fir mixture, similarly to the control stand.

Areas damaged by stand-replacing disturbances usually act as carbon sources for some years (Thuiller et al., 2000). In forest damaged by wind or avalanche, unlike wildfires, no CO_2 is directly released in the atmosphere during the disturbance event. However, even without consumption of organic matter (such as during wildfire) or removal by salvage logging or gravity (as may be the case of the recently disturbed site), the biomass transferred from live to dead pools is subject to microbial decomposition and quickly loses carbon while decomposing (Liu et al., 2011). Finally, the avalanche can remove soil carbon by mechanical elimination of the upper soil layers (Confortola et al., 2012; Korup and Rixen, 2014). However, in our study area the recently disturbed site preserved a significant amount of soil carbon (78 Mg ha^{-1} on average), most of which was stocked in soil. The lower C/N ratio in soils of the avalanche track indicated a higher fertility and slower C turnover, likely due to the prolonged permanence of snow and higher soil moisture.

We did not measure C fluxes, therefore the release of C from the recently disturbed site is unknown. More studies are needed to ascertain how much carbon is released following avalanche disturbances at the site and regional scale, and if and how long it takes for the post-disturbance vegetation to stock as much carbon as to equate the losses. The overall carbon balance can still be positive if losses in areas disturbed by avalanches are counteracted by mature and old-age forests serving as sinks in undisturbed areas between avalanche tracks.

Plant diversity

Plant diversity has long been related to disturbance frequency and severity, i.e., in the framework of the (much debated) intermediate disturbance hypothesis (IDH) (Connell, 1978; Fox, 2013). In our study, we found that the active avalanche track had the highest species richness and diversity (Shannon index, although not significantly). This is in contrast with the IDH, but in accordance with previous research on the effect of disturbances on plant diversity in mountain forests, and particularly avalanches (Ilisson et al., 2006; Rixen et al., 2007; Fischer et al., 2012).

The plant community of the avalanche track can be described as a true avalanche grassland (Erschbamer, 1989), with species belonging to typical avalanche grasslands (*Molinio-Arrhenateretea*) and to the adjacent mountain meadows (e.g., *Trisetum flavescens*). High richness in the avalanche track can be explained by (1) gravitational transport of propagules of plants from higher elevations (Erschbamer, 1989); (2) increased habitat diversity due to the mosaic of areas with prolonged snow cover, eroded soil patches, or running melt water (Rixen and Brugger, 2004); (3) newly created forest edges (Duelli et al., 2002); (4) disturbance legacies (Franklin et al., 2002) such as coarse woody debris, pit-and-mound topography, and the mosaic of open areas and living legacies such as resprouting broadleaves (Rixen et al., 2007). Therefore, the maintenance of a periodically disturbed portion of the land is be beneficial for overall species richness and diversity, facilitating the persistence of more light-demanding, early-seral species (Lonati et al., 2013).

Previous research found that the shift from shrub- to tree- dominated vegetation occurred when the average interval between avalanches was 15-20 years (Johnson, 1987). Plant communities of the old disturbance and control sites were very similar, and shared many species from both the *Piceetalia* and the *Fagetalia* classes. Consistently to our study, previous research found that strong changes in species composition result from multiple avalanche occurrences, rather than single events that affect the forest structure heavily but may not result in sufficient changes in soil microclimate and mechanical disturbance (Fischer et al., 2012).

If we focus on the study site as a unique ecosystem, we notice that only one-third of the total number of species found was common to all disturbance treatments, i.e., the total species richness was higher than in any individual disturbance treatment. The mosaic of disturbed and undisturbed patches allows for coexistence of both early-seral, open-field species, and shade-tolerant species under or in the vicinity of the tree and shrub canopies. Further research is needed to ascertain if this diversity effects occur in other taxa, e.g., invertebrates, fungi, or lichens. Coarse wood debris, a commonly used metric of diversity for forest biota (Bouget and Duelli, 1994), was higher in the control forest than in the avalanche track; however, management in the former, and diversity of microsites in the latter, act as confounding variables, and could mitigate or even invert the simplistic relationship between disturbance frequency, CWD, and invertebrate diversity (e.g., Negro et al., 2014).

Ungulate habitat

As ungulates use resources very differently during the year, it is difficult to condensate habitat suitability in a single, static metric. We chose to use three different proxies for ungulate habitat: hiding cover, expressed as a function of tree density and size (Smith and Long, 1987); summer food availability, expressed by herb and shrub cover as a proxy (Moser et al., 2008), and winter food availability, expressed by measured browsing intensity on tree regeneration and shrubs. The use of browsing index alone would in fact underestimate habitat suitability of open areas dominated by herb cover such as those in or near the avalanche track.

Logically, herb and shrub cover were much more abundant in open, recently disturbed sites (Krojerová-Prokešová et al., 2010). However, these lacked the necessary hiding requirements due to low or non-existent tree cover, and were also less used during winter – probably due to scarce food and high snow cover. In fact, browsing on trees and shrubs was more severe in the control site – even if treatment effect was weak, probably due to the fact that distance between sampling plots was well within the daily movement capabilities of individual ungulates (Pépin et al., 2004). Browsing can affect future species composition of the forest (Motta 1996); in the study area, this effect could be important for Silver fir (Klopcic et al., 2010), which is highly palatable and, at the same time, not so abundant in the regeneration layer (Table 3). The

In past studies, the optimal habitat for red deer and roe deer has been described as a mixture of open meadows and closed canopy, rich in forest edges so as to provide both food and shelter to the animals (Hanley, 1984; Gill et al., 1996; Licoppe, 2006). In areas hit by natural disturbance, coarse woody debris could also alter ungulate frequentation and feeding behavior. The effect of CWD on ungulate habitat use could be either positive – by stabilizing the snowpack, facilitating animal movement when snow is on the ground, or by the fact that saplings emerging from CWD are more readily visible by the deer (Pellerin et al., 2010) – or negative, if the abundance, size and spatial arrangement of CWD is such as to impair animal movement and feeding (Kupferschmid and Bugmann, 2005; de Chantal and Granström, 2007). We did not observe any site where this latter condition could be the case.

Protection from rockfall

Concerning protection against hazards, we assessed the effectiveness of the forest in stopping falling rocks of different size and preventing them from reaching the village and roads downslope (Fig. 1). The managed forest is currently effective against rockfall. On the contrary, the (almost treeless) avalanche track is certainly not effective for rockfall protection, but any falling rock would be channeled within its steep banks and end up in the river below. The minimum required basal area for this slope is 20 m^2 ha^{-1} to reach a PRH of 95% for moderate sized rocks (RockforNET results). In the recent disturbance site, or in the eventuality of a new avalanche event as severe as the 1959 one, actions to mitigate the rockfall hazard should be carried out if the rockfall protection service is prioritized (e.g., rockfall nets or temporary log fences).

More interestingly, the old disturbance stand is currently very effective against rockfall protection (PRH: 99% for moderate-sized rocks, and 83% for large rocks), mainly because of the high density of stems, which may act as a fence blocking falling rocks (Gsteiger, 1993; Vacchiano et al., 2008; Jancke et al., 2009).

Conclusions

In order to maintain or replenish the provision of ecosystem services in the face of natural disturbances, managers need to understand the relationship between disturbance frequency, intensity, and the duration and magnitude of the consequent changes in ecosystem service provision.

This study assessed changes in ecosystem services provided by a spruce-fir mountain forest disturbed by avalanches, by comparing carbon stock, plant diversity, ungulate habitat, and protection against rockfall in stands experiencing zero, one, and multiple disturbance events. We showed that: (1) high disturbance frequencies are beneficial for plant diversity, (2) after 50 years the forest was optimal for rockfall protection, and (3) the regularly managed forest had the highest carbon stocks.

Avalanches are a source of patchiness and habitat heterogeneity. Once safety of households and roads is ensured, the maintenance of a share of the landscape disturbed by avalanches of variable size, magnitude and frequency can be beneficial to several ecosystem services, such as biodiversity and wildlife habitat. Carbon losses due to disturbances can be offset by enhanced conservation of mature and old-aged forests in undisturbed areas. Elucidating tradeoffs between ecosystem service provision and disturbance frequency will help managers in planning management actions (e.g., avalanche suppression) and distribute them across the landscape according to the ecosystem services to prioritize.

Acknowledgements

We acknowledge Luisella Celi for soil analyses, Michele Lonati for plant determination, Corpo Forestale Regionale and Ufficio Neve e Valanghe - Regione Autonoma Valle d'Aosta for data provision.

References

Aeschimann D, Lauber K, Moser MD, Theurillat JP (2004) Flora Alpina. Zanichelli, Bologna

Bebi P, Kulakowski D, Rixen C (2009) Snow avalanche disturbances in forest ecosystems—State of research and implications for management. For Ecol Manage 257:1883–1892.

Bellassen V, Viovy N, Luyssaert S, Maire G, Schelhaas MJ, Ciais P (2011) Reconstruction and attribution of the carbon sink of European forests between 1950 and 2000. Glob Change Biol 17:3274–3292.

Berger F, Dorren L (2007) Principles of the tool Rockfor.net for quantifying the rockfall hazard below a protection forest. Schweiz Z Forstwes 158:157–165.

Berger F, Rey F (2004) Mountain protection forests against natural hazards and risks: new French developments by integrating forests in risk zoning. Nat Hazards 33:395–404.

Berger TW, Neubauer C, Glatzel G (2002) Factors controlling soil carbon and nitrogen stores in pure stands of Norway spruce (Picea abies) and mixed species stands in Austria. For Ecol Manage 159:3–14.

Bigot C, Dorren LKA, Berger F (2008) Quantifying the protective function of a forest against rockfall for past, present and future scenarios using two modelling approaches. Nat Hazards 49:99–111. doi: 10.1007/s11069-008-9280-0

Black H, Scherzinger RJ, Thomas JW (1976) Relationship of Rocky Mountain Elk and Rocky Mountain Mule Deer to Timber Management in the Blue Mountains of Oregon and Washington. In: Hieb SR (ed), Proceedings of the Elk-Logging-Roads Symposium. University of Idaho, Moscow, pp. 11-35.

Bond-Lamberty B, Wang C, Gower ST (2004) Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Glob Change Biol 10:473–487. doi: 10.1111/j.1529-8817.2003.0742.x

Børset O (1960) Silviculture of aspen. Scottish For 14:68–80.

Bottero A, Garbarino M, Long JN, Motta R (2013) The interacting ecological effects of large-scale disturbances and salvage logging on montane spruce forest regeneration in the western European Alps. For Ecol Manage 292:19–28.

Bouget C, Duelli, P (2004) The effects of windthrow on forest insect communities: a literature review. Biological Conservation 118:281-299.

Boulanger V, Baltzinger C, Saïd S, Ballon P, Picard J-F, Dupouey J-L (2009) Ranking temperate woody species along a gradient of browsing by deer. For Ecol Manage 258:1397–1406. doi: 10.1016/j.foreco.2009.06.055

Brang P (2001) Resistance and elasticity: Promising concepts for the management of protection forests in the European Alps. For Ecol Manage 145:107–119.

Brang P, Schonenberger W, Schwitter R, Wasser B (2006) Management of protection forests in the European Alps: an overview. For Snow Landsc Res 80:23–44.

Briner S, Huber R, Bebi P, Elkin C, Schmatz DR, Grêt-Regamey A (2013) Trade-Offs between Ecosystem Services in a Mountain Region. Ecology and Society 18:art35. doi: 10.5751/ES-05576-180335

Brotons L, Aquilué N, De Cáceres M, Fortin M-J, Fall A (2013) How fire history, fire suppression practices and climate change affect wildfire regimes in Mediterranean landscapes. PLoS One 8:e62392. doi: 10.1371/journal.pone.0062392.s004

Bullock JM, Aronson J, Newton AC, Pywell RF, Rey-Benayas JM (2011) Restoration of ecosystem services and biodiversity: conflicts and opportunities. Trends in Ecology and Evolution 26:541–549. doi: 10.1016/j.tree.2011.06.011

Butler DR (1985) Vegetational and geomorphic change on snow avalanche paths, Glacier National Park, Montana, USA. Western North American Naturalist 45:313–317.

Butler DR (2001) Geomorphic process-disturbance corridors: a variation on a principle of landscape ecology. Progress Physical Geogr 25:237–238. doi: 10.1177/030913330102500204

Camerano P, Terzuolo PG, Varese P (2007) I tipi forestali della Valle d'Aosta. Compagnia delle Foreste, Arezzo

Castellani C, Scrinzi G, Tabacchi G, Tosi V (1984) Inventario Forestale Nazionale Italiano (IFNI): tavole di cubatura a doppia entrata. Ministero dell'Agricoltura e delle Foreste, Trento

Chemini C, Rizzoli A (2003) Land use change and biodiversity conservation in the Alps. Journal of Mountain Ecology 7:1–7.

Ciais P, Schelhaas MJ, Zaehle S, Piao S, Cescatti A, Liski J, Luyssaert S, Le Maire G, Schulze ED, Bouriaud O (2008) Carbon accumulation in European forests. Nature Geosci 1:425–429.

Condé S, Richard D, Liamine N, Leclère A-S, Sotolargo B, Pinborg U, Larsson TB, Svensson L (2006) Europe’s biodiversity - The Alpine region. European Environment Agency, Bruxelles

Confortola G, Maggioni M, Freppaz M, Bocchiola D (2012) Modelling soil removal from snow avalanches: A case study in the North-Western Italian Alps. Cold Regions Science and Technology 70:43–52. doi: 10.1016/j.coldregions.2011.09.008

Connell JH (1978) Diversity in Tropical Rain Forests and Coral Reefs. Science 199:1302–1310. doi: 10.1126/science.199.4335.1302

Conti G, Fagarazzi L (2004) Sustainable Mountain Development and the key - issue of Abandonment of Marginal Rural Areas. Planum 11:1–20.

Cordonnier T, Berger F, Elkin C, Lämås T, Martinez M (2013) Models and linker functions (indicators) for ecosystem services. [Online document] URL: www.arange-project.eu/wp-content/uploads/ARANGE-D2.2_linkerfunctions.pdf. Last accessed: February 16, 2015.

de Chantal M, Granström A (2007) Aggregations of dead wood after wildfire act as browsing refugia for seedlings of Populus tremula and Salix caprea. For Ecol Manage 250:3–8. doi: 10.1016/j.foreco.2007.03.035

Dorren LKA, Maier B, Putters US, Seijmonsbergen AC (2004) Combining field and modelling techniques to assess rockfall dynamics on a protection forest hillslope in the European Alps. Geomorphol 57:151–167. doi: 10.1016/S0169-555X(03)00100-4

Duelli P, Obrist MK, Fluckiger PF (2002) Forest edges are biodiversity hotspots–also for Neuroptera. Acta Zoologica Academiae Scientiarum Hungaricae 48:75–87.

Elkin C, Gutiérrez AG, Leuzinger S, Manusch C, Temperli C, Rasche L, Bugmann H (2013) A 2 °C warmer world is not safe for ecosystem services in the European Alps. Glob Change Biol 19:1827–1840.

Erschbamer B (1989) Vegetation on avalanche paths in the Alps. Vegetatio 80:139–146.

Faccoli M, Stergulc F (2004) Ips typographus (L.) pheromone trapping in south Alps: spring catches determine damage thresholds. J Appl Entomol 128:307–311. doi: 10.1111/j.1439-0418.2004.00848.307–311

Falcucci A, Maiorano L, Boitani L (2006) Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. Landsc Ecol 22:617–631. doi: 10.1007/s10980-006-9056-4

Fischer A, Fischer H, Lehnert U (2012) Avalanches creating high structural and floristic diversity in mountain mixed forests in the Alps. Biodiv Conserv 21:643–654.

Fox JW (2013) The intermediate disturbance hypothesis should be abandoned. Trends in Ecology and Evolution 28:86–92. doi: 10.1016/j.tree.2012.08.014

Franklin JF, Spies TA, Pelt RV, Carey AB, Thornburgh DA, Berg DR, Lindenmayer DB, Harmon ME, Keeton WS, Shaw DC (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For Ecol Manage 155:399–423.

Frehner M, Wasser B, Schwitter R (2005) Nachhaltigkeit und Erfolgskontrolle Im Schutzwald. Wegleitung für Pflegemassnahmen in Wäldern mit Schutzfunktion. Bundesamt für Forstwesen und Landschaftsschutz, Bern

Gill RMA, Johnson AL, Francis A, Hiscocks K, Peace AJ (1996) Changes in roe deer (Capreolus capreolus L.) population density in response to forest habitat succession. For Ecol Manage 88:31–41. doi: 10.1016/S0378-1127(96)03807-8

Gimmi U, Wolf A, Bürgi M, Scherstjanoi M, Bugmann H (2008) Quantifying disturbance effects on vegetation carbon pools in mountain forests based on historical data. Reg Environ Change 9:121–130. doi: 10.1007/s10113-008-0071-7

Gleixner G, Tefs C, Jordan A, Hammer M, Wirth C, Nueske A, Telz A, Schmidt UE, Glatzel S (2009) Soil carbon accumulation in old-growth forests. In: Wirth C, Gleixner G, Heimann M (eds) Old growth forests. Function, fate, value. Springer, Berlin, pp 231–266.

Goodale CL, Apps MJ, Birdsey RA, Field CB, Heath LS, Houghton RA, Jenkins JC, Kohlmaier GH, Kurz W, Liu S (2002) Forest carbon sinks in the Northern Hemisphere. Eco App 12:891–899.

Gough CM, Vogel CS, Harrold KH, George K, Curtis PS (2007) The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest. Glob Change Biol 13:1935–1949. doi: 10.1111/j.1365-2486.2007.01406.x

Grêt-Regamey A, Bebi P, Bishop ID, Schmid WA (2008b) Linking GIS-based models to value ecosystem services in an Alpine region. J Environ Manage 89:197–208. doi: 10.1016/j.jenvman.2007.05.019

Grêt-Regamey A, Brunner SH, Altwegg J, Christen M, Bebi P (2013) Integrating Expert Knowledge into Mapping Ecosystem Services Trade-offs for Sustainable Forest Management. Ecology and Society 18:art34. doi: 10.5751/ES-05800-180334

Grêt-Regamey A, Walz A, Bebi P (2008a) Valuing Ecosystem Services for Sustainable Landscape Planning in Alpine Regions. Mt Res Dev 28:156–165. doi: 10.1659/mrd.0951

Gsteiger P (1993) Steinschlagschutzwald - Ein Beitrag zur Abgrenzung, Beurteilung und Bewirtschaftung. Schweiz Z Forstwes 144:115–132.

Haines-Young R, Potschin M, Kienast F (2012) Indicators of ecosystem service potential at European scales: Mapping marginal changes and trade-offs. Ecol Indic 21:39–53.

Hanley TA (1984) Relationships between Sitka black-tailed deer and their habitat. Gen Tech Rep PNW-168. USDA Forest Service, Pacific Northwest Research Station, Portland OR.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978. doi: 10.1002/joc.1276

Ilisson T, Metslaid M, Vodde F, Jogiste K, Kurm M (2006) Vascular plant response to windthrow severity in Norway spruce–dominated Myrtillus site type forests in Estonia. Ecoscience 13:193–202. doi: 10.2980/i1195-6860-13-2-193.1

Jancke O, Dorren LK, Berger F, Fuhr M, Kohl M (2009) Implications of coppice stand characteristics on the rockfall protection function. For Ecol Manage 259:124–131. doi: 10.1016/j.foreco.2009.10.003

Jandl R, Lindner M, Vesterdal L, Bauwens B, Baritz R, Hagedorn F, Johnson DW, Minkkinen K, Byrne KA (2007) How strongly can forest management influence soil carbon sequestration? Geoderma 137:253‑268.

Johnson EA (1987) The relative importance of snow avalanche disturbance and thinning on canopy plant populations. Ecology 68:43–53.

Klopcic M, Jerina K, Boncina A (2010) Long-term changes of structure and tree species composition in Dinaric uneven-aged forests: are red deer an important factor? Eur J For Res 129:277–288.

Korup O, Rixen C (2014) Soil erosion and organic carbon export by wet snow avalanches. The Cryosphere Discuss 8:1–19. doi: 10.5194/tcd-8-1-2014

Krojerová-Prokešová J, Barančeková M, Šustr P, Heurich M (2010) Feeding patterns of red deer Cervus elaphus along an altitudinal gradient in the Bohemian Forest: effect of habitat and season. Wildlife Biol 16:173–184. doi: 10.2981/09-004

Krug J, Koehl M, Kownatzki D (2012) Revaluing unmanaged forests for climate change mitigation. Carbon Balance Manage 7:11.

Kulakowski D, Rixen C, Bebi P (2006) Changes in forest structure and in the relative importance of climatic stress as a result of suppression of avalanche disturbances. For Ecol Manage 223:66–74. doi: 10.1016/j.foreco.2005.10.058

Kupferschmid AD, Bugmann H (2005) Effect of microsites, logs and ungulate browsing on Picea abies regeneration in a mountain forest. For Ecol Manage 205:251–265. doi: 10.1016/j.foreco.2004.10.008

Laiolo P, Rolando A, Valsania V (2004) Responses of birds to the natural re-establishment of wilderness in montane beechwoods of North-western Italy. Acta Oecol 25:129–136. doi: 10.1016/j.actao.2003.12.003

Lal R (2005) Forest soils and carbon sequestration. For Ecol Manage 220:242–258. doi: 10.1016/j.foreco.2005.08.015

Licoppe AM (2006) The diurnal habitat used by red deer (Cervus elaphus L.) in the Haute Ardenne. Eur J Wildl Res 52:164–170. doi: 10.1007/s10344-006-0027-5

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolström M, Lexer MJ, Marchetti M (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For Ecol Manage 259:698–709.

Liu S, Bond-Lamberty B, Hicke JA, Vargas R, Zhao S, Chen J, Edburg SL, Hu Y, Liu J, McGuire AD, Xiao J, Keane R, Yuan W, Tang J, Luo Y, Potter C, Oeding J (2011) Simulating the impacts of disturbances on forest carbon cycling in North America: Processes, data, models, and challenges. J Geophys Res 116:G00K08. doi: 10.1029/2010JG001585

Lonati M, Vacchiano G, Berretti R, Motta R (2013) Effect of stand-replacing fires on Mediterranean plant species in their marginal alpine range. Alp Botany, in press. doi: 10.1007/s00035-013-0115-6

Lunardi S, Freppaz M, Debernardi A, Segor V (2009) Il nuovo catasto valanghe in Valle d'Aosta. Neve e Valanghe 66:16–23.

Luyssaert S, Schulze ED, Bőrner A, Knohl A, Hessenmőller D, Law BE, Ciais P, Grace J (2008) Old-growth forests as global carbon sinks. Nature 455:211–213.

Magurran AE (1988) Ecological Diversity and its Measurement. Princeton University Press, Princeton.

Meloni F, Lingua E, Motta R (2006) Analisi della funzione protettiva delle foreste: l'esempio della "Carta delle foreste di protezione diretta della Valle d'Aosta". Forest@ 3:420–425.

Metzger MJ, Rounsevell MDA, Acosta-Michlik L, Leemans R, Schröter D (2006) The vulnerability of ecosystem services to land use change. Agric Ecosyst Environ 114:69–85.

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: Current state and trends. Island Press, Washington DC.

Moser B, Schütz M, Hindenlang KE (2008) Resource selection by roe deer: Are windthrow gaps attractive feeding places?. For Ecol Manage 255:1179-1185.

Motta R (1996) Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the Western Italian Alps. For Ecol Manage 88:93–98. doi: 10.1016/S0378-1127(96)03814-5

Motta R., Edouard JL (2005) Stand structure and dynamics in a mixed and multilayered forest in the Upper Susa Valley, Piedmont, Italy. Can J For Res 35:21-36.

Motta R, Garbarino M, Berretti R, Meloni F, Nosenzo A, Vacchiano G (2015) Development of old-growth characteristics in uneven-aged forests of the Italian Alps. Eur J For Res 134:19-31.

Motta R, Haudemand J-C (2000) Protective forests and silvicultural stability - An example of planning in the Aosta Valley. Mt Res Dev 20:180–187.

Nave LE, Vance ED, Swanston CW, Curtis PS (2010) Harvest impacts on soil carbon storage in temperate forests. For Ecol Manage 259:857–866

Negro M, Vacchiano G, Berretti R, Chamberlain DE, Palestrini C, Motta R, Rolando A (2014) Effects of forest management on ground beetle diversity in alpine beech (*Fagus sylvatica* L.) stands. For Ecol Manage 328:300-309.

Nelson E, Mendoza G, Regetz J, Polasky S, Tallis H, Cameron D, Chan KM, Daily GC, Goldstein J, Kareiva PM, Lonsdorf E, Naidoo R, Ricketts TH, Shaw M (2009) Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Frontiers Ecol Environ 7:4–11. doi: 10.1890/080023

Niedrist G, Tasser E, Lüth C, Dalla Via J, Tappeiner U (2008) Plant diversity declines with recent land use changes in European Alps. Plant Ecology 202:195–210. doi: 10.1007/s11258-008-9487-x

Nilsen P, Strand LT (2013) Carbon stores and fluxes in even- and uneven-aged Norway spruce stands. Silva Fennica 47:1024.

Nosenzo A (2005) Sistemi di tariffe per la cubatura delle principali conifere della Regione Valle d'Aosta. In: Caivano F, Girardi T, Pierangeli D, Borghetti M (eds) Atti del IV congresso nazionale della Società Italiana di Selvicoltura e Ecologia Forestale. Rifreddo (PZ), 7-10 October 2003. S.I.S.E.F, Potenza, pp 209–213

Ohmann LF, Grigal DF, Brander RB (1976) Biomass estimation for five shrubs from northeastern Minnesota. USDA Forest Service, North Central Forest Experiment Station, St. Paul MN

Olschewski R, Bebi P, Teich M, Wissen Hayek U, Grêt-Regamey A (2012) Avalanche protection by forests — A choice experiment in the Swiss Alps. For Policy Econ 17:19-24

Ozenda P, Borel JL (1994) Biocoenotic diversity patterns in the alpine belt of the mountains in Western and Central Europe. Colloques Phytosoc 23:723–735

Pearson T, Brown SL, Birdsey RA (2007) Measurement guidelines for the sequestration of forest carbon. USDA Forest Service, Northern Research Station, Newtown Square PA

Pellerin M, Saïd S, Richard E, Hamann J-L, Dubois-Coli C, Hum P (2010) Impact of deer on temperate forest vegetation and woody debris as protection of forest regeneration against browsing. For Ecol Manage 260:429–437. doi: 10.1016/j.foreco.2010.04.031

Pellissier L, Pinto-Figueroa E, Niculita-Hirzel H, Moora M, Villard L, Goudet J, Guex N, Pagni M, Xenarios I, Sanders I, Guisan A (2013) Plant species distributions along environmental gradients: do belowground interactions with fungi matter? Frontiers in Plant Science 4:500. doi: 10.3389/fpls.2013.00500

Penman J, Gytarsky M, Hiraishi T, Krug T, Kruger D, Pipatti R, Buendia L, Miwa K, Ngara T, Tanabe K, Wagner F (2003) Definitions and methodological options to inventory emissions from direct human-induced degradation of forests and devegetation of other vegetation types. Institute for Global Environmental Strategies, Hayama

Pépin D, Adrados C, Mann C, Janeau G (2004) Assessing real daily distance traveled by ungulates using differential GPS locations. Journal of Mammalogy 85:774–780. doi: 10.1644/BER-022

Perello P, Piana F, Martinotti G (1999) Neo-Alpine structural features at the boundary between the Penninic and Helvetic domains (Prè S. Didiér-Entrèves, Aosta valley, Italy). Eclogae Geol Helv 92:347-359.

Pothier D, Raulier F, Riopel M (2004) Ageing and decline of trembling aspen stands in Quebec. Can J For Res 34:1251–1258.

Pötzelsberger E, Hasenauer H (2015) Soil change after 50 years of converting Norway spruce dominated age class forests into single tree selection forests. For Ecol Manage 388:176-182.

Pregitzer KS, Euskirchen ES (2004) Carbon cycling and storage in world forests: biome patterns related to forest age. Glob Change Biol 10:2052–2077. doi: 10.1111/j.1365-2486.2004.00866.x

Reichelt G, Wilmanns O (1973) Vegetationsgeographie. Georg Westermann, Braunschweig

Richter DD, Markewitz D, Trumbore SE, Wells CG (1999) Rapid accumulation and turnover of soil carbon in a re-establishing forest : Abstract : Nature. Nature 400:56–58. doi: 10.1038/21867

Rigling A, Bigler C, Eilmann B, Feldmeyer-Christe E, Gimmi U, Ginzler C, Graf U, Mayer P, Vacchiano G, Weber P, Wohlgemuth T, Zweifel R, Dobbertin M (2013) Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Glob Change Biol 19:229–240. doi: 10.1111/gcb.12038

Rixen C, Brugger S (2004) Naturgefahren – ein Motor der Biodiversität. Forum für Wissen 2004:67–71.

Rixen C, Haag S, Kulakowski D, Bebi P (2007) Natural avalanche disturbance shapes plant diversity and species composition in subalpine forest belt. J Veg Sci 18:735–742.

Rytter L, Stener LG (2005) Productivity and thinning effects in hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) stands in southern Sweden. Forestry 78:285–295.

Smith FW, Long JN (1987) Elk hiding and thermal cover guidelines in the context of lodgepole pine stand density. West J Appl For 2:6-10.

Spencer KL, Harvey GL (2012) Understanding system disturbance and ecosystem services in restored saltmarshes: Integrating physical and biogeochemical processes. Estuarine, Coastal and Shelf Science 106:23–32. doi: 10.1016/j.ecss.2012.04.020

Stokes MA, Smiley TL (1996) An introduction to tree-ring dating. University of Chicago Press, Chicago

Teich M, Bebi P (2009) Evaluating the benefit of avalanche protection forest with GIS-based risk analyses—A case study in Switzerland. For Ecol Manage 257:1910–1919. doi: 10.1016/j.foreco.2009.01.046

Teich M, Fischer J-T, Feistl T, Bebi P, Christen M, Grêt-Regamey A (2013) Computational snow avalanche simulation in forested terrain, Nat Hazards Earth Syst Sci Discuss 1:5561-5601. doi:10.5194/nhessd-1-5561-2013

Thornton PE, LAW BE, Gholz HL, Clark KL, Falge E, Ellsworth DS, Goldstein AH, Monson RK, Hollinger D, Falk M (2002) Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. Agric For Meteorol 113:185–222.

Thuille A, Buchmann N, Schulze ED (2000) Carbon stocks and soil respiration rates during deforestation, grassland use and subsequent Norway spruce afforestation in the Southern Alps, Italy. Tree Physiol 20:849–857.

Ulbrich U, Fink AH, Klawa M, Pinto JG (2001) Three extreme storms over Europe in December 1999. Weather 56:70–80.

Vacchiano G, Motta R, Long JN, Shaw JD (2008) A density management diagram for Scots pine (Pinus sylvestris L.): A tool for assessing the forest's protective effect. For Ecol Manage 255:2542–2554. doi: 10.1016/j.foreco.2008.01.015

Veraverbeke S, Verstraeten WW, Lhermitte S, Goossens R (2010) Evaluating Landsat Thematic Mapper spectral indices for estimating burn severity of the 2007 Peloponnese wildfires in Greece. Int J Wildl Fire 19:558-569. doi: 10.1071/WF09069

Viglietti D, Letey S, Motta R, Maggioni M, Freppaz M (2010) Snow avalanche release in forest ecosystems: A case study in the Aosta Valley Region (NW-Italy). Cold Regions Sci Technol 64:167–173.

Walther P (1986) Land abandonment in the Swiss Alps: a new understanding of a land-use problem. Mt Res Dev 6:305. doi: 10.2307/3673371

Wehrli A, Brang P, Maier B, Duc P, Binder F, Lingua E, Ziegner K, Kleemayr K, Dorren L (2007) Management of protection forests in the Alps – an overview. Schweiz Z Forstwes 158:142–156. doi: 10.3188/szf.2007.0142

Zhou G, Liu SG, Li Z, Zhang D, Tang X, Zhou C, Yan J, Mo J (2006) Old-growth forests can accumulate carbon in soils. Science 314:1417.

Tables

Table 1 Parameters for the calculation of stand biomass (from Vitullo et al., 2007)

Cover type	**Biomass Expansion Factor**	**Dry:fresh weight**	**Root:shoot ratio**
Conifers	1.29	0.38	0.29
Broadleaves	1.47	0.53	0.24
Shrubs	1.44	0.52	0.42

Table 2 Parameters of the allometric equations for shrub biomass (from Ohmann et al., 1976)

Species	**x**	**parameter**	**twig biomass**	**stem biomass**	**total biomass**
Corylus avellana	stem height	a	0.003268	0.00002089	0.0002791
		b	1.373	2.98	2.52
Lonicera spp.	crown area	a	0.0819	0.7513	-
		b	0.6072	0.625	-
Other shrubs	crown area	a	0.3504	0.8201	-
		b	0.2888	0.577	-

Table 3 Species palatability scores, mean browsing damage (0: none, 6: 100% browsed), and average per hectare frequency of regeneration and shrubs in the three observation sites. Only species where 10 or more individuals were samples are included.

			Average per hectare frequency		
Species	Palatability	Mean browsing damage	Control	Old disturbance	Recent disturbance
Abies alba	0.8	4.7	799	561	1249
Acer spp.	0.9	1.4	311	130	26141
Berberis vulgaris	0.05	1.1	76	229	3333
Betula pendula	0.3	0.5	1469	4047	66643
Corylus avellana	0.7	2.5	446	803	66667
Fraxinus excelsior	0.9	0.9	183	630	90848
Lonicera spp.	0.6	2.0	1516	3210	206667
Picea abies	0.3	0.4	708	399	4444
Populus tremula	0.4	1.7	0	58	6780
Salix spp.	0.6	1.5	247	333	154544
Sorbus spp.	0.6	1.1	725	185	730
Rosa spp.	0.1	2.2	25	13	2222
Rubus spp.	0.6	1.1	13	64	148889

Table 4 Summary of stand structural variables in the control, old, and recent avalanche sites

		Control		Old disturbance		Recent disturbance	
Variable	**Units**	**mean**	**SE**	**mean**	**SE**	**mean**	**SE**
Basal area	$m^2 ha^{-1}$	56.1	12.02	46.9	5.61	6.5	1.70
Tree density	ha^{-1}	1763	270.9	3961	658.3	2065	406.4
QMD	cm	20.8	2.17	12.8	0.59	6.0	0.40
Mean height	m	13.7	0.72	10.4	0.31	4.6	0.37
Tree volume	$m^3 ha^{-1}$	527.3	48.81	372.0	33.53	20.5	7.03
CWD volume	$m^3 ha^{-1}$	35.6	17.25	21.4	5.84	6.6	2.89
Mean age	years	64	3.7	45	2.6	24	2.4
Basal area by spruce	%	53	7.4	37	5.9	1	0.9
Basal area by fir	%	27	9.5	6	2.0	1	0.1
Basal area by larch	%	5	3.5	3	2.6	1	0.6
Basal area by broadleaves	%	9	2.5	54	6.9	98	1.2
Tree cover	%	57	5.8	69	4.5	12	3.7
Shrub cover	%	13	2.5	15	4.7	53	8.2
Herb cover	%	5	1.0	4	1.1	48	7.6
Bare soil	%	3	0.8	3	1.3	3	1.1
Regeneration[a] density	ha^{-1}	10309	4232.5	4039	2422.0	8342	3590.0
Regeneration[a] by spruce	%	18	6.5	8	4.3	1	1.1
Regeneration[a] by broadleaves	%	53	11.8	75	10.0	98	1.4

[a] Regeneration: H >10 cm, DBH <2.5 cm

Table 5 Summary of ecosystem service values in the control, old, and recent avalanche sites. Sites marked by similar letters did not differ significantly (Kruskal-Wallis test, $p > 0.05$)

		Control		Old disturbance		Recent disturbance	
Variable	**Units**	**mean**	**SE**	**mean**	**SE**	**mean**	**SE**
Herb+shrub cover (summer resource)	%	11 **a**	1.6	10 **a**	3.1	58 **b**	6.5
Browsing index (winter resource)	%	38 **a**	5.4	21 **b**	5.4	26 a**b**	4.7
Elk hiding cover	%	95 **a**	0.9	99 **a**	0.1	29 **b**	12.2
Total C	Mg ha^{-1}	402 **a**	30.1	222 **b**	26.2	64 **c**	11.8
Shannon index	-	1.5 **a**	0.12	1.6 **a**	0.12	2.1 **a**	0.41
Evenness	-	0.7 **a**	0.04	0.8 **a**	0.05	0.7 **a**	0.12
PRH (moderate size rocks)	%	95 **a**	5.2	99 **a**	2.3	11 **b**	6.7
PRH (large size rocks)	%	74 **a**	6.4	83 **b**	3.3	5 **c**	2.1

Figure captions

Fig. 1 Study area location, maximum avalanche perimeter from the regional avalanche cadaster (CRV) and sampling design. Colored perimeters represent several occurrences of the avalanche as recorded by CRV. White dots: recent avalanche site; grey dots: old avalanche site; black dots: control site.

Fig. 2 The avalanche event in 1959 (a) and 2009 (b), with indication of the control (C), old (O), and recent (R) avalanche sites. Image (a) by Ufficio Neve e Valanghe - Regione Autonoma Valle d'Aosta, (b) by the authors.

Fig. 3 Observed stand structure parameters in plots from the control (C), old (O), and recent (R) avalanche sites

Fig. 4 DBH (frequency distribution) and age (smoothed relative frequency distribution) in the control, old, and recent avalanche sites

Fig. 5 Individual tree DBH-age models for spruce (PA), silver fir (AA), birch (BP), aspen (PT) and other broadleaves (OB) in the study area (dendrochronological subsample, all treatments pooled). Model form was age = a + b DBH

Fig. 6 Scatterplot of tree ages (all species – both measured and modeled tree age) in all sampling plots from the control (C), old (O) and recent (R) avalanche sites

Fig. 7 Carbon stocks [Mg ha^{-1}] by ecosystem component in the control (C), old (O), and recent (R) avalanche sites. Sites marked by similar letters did not differ significantly (Kruskal-Wallis test, $p > 0.05$)

Fig. 8 Photographs taken during field sampling in the control (a), old (b), and recent (c) avalanche sites. Images by the authors.

Supplementary material S1

Species list and abundance scores (Braun-Blanquet, 1932) for the regeneration, shrub, and herbaceous layers of the control site, the old disturbance, and the more recently disturbed site.

Figure 1

Click here to download high resolution image

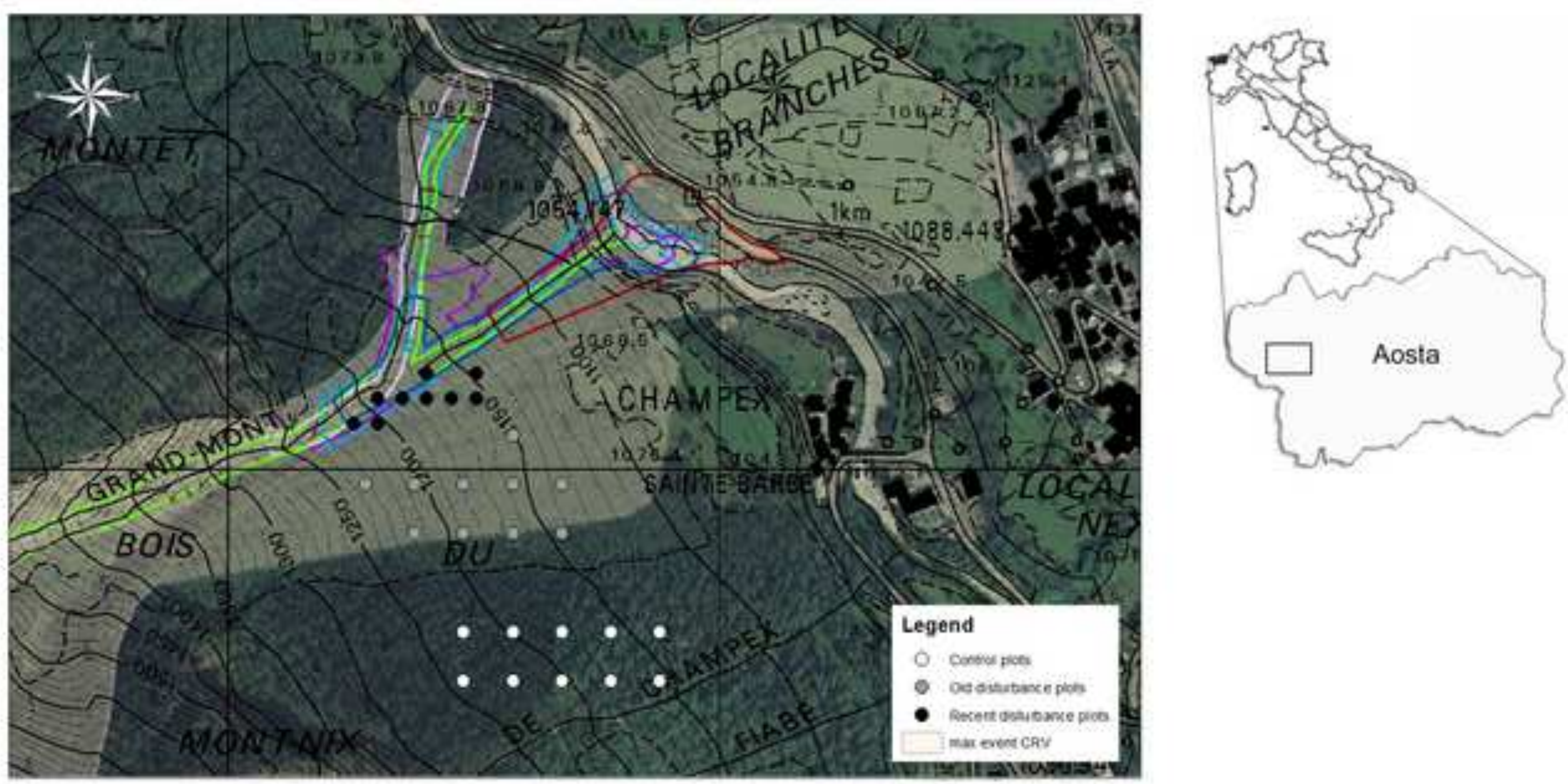

Figure 2a
Click here to download high resolution image

Figure 2b
Click here to download high resolution image

Figure 3
Click here to download high resolution image

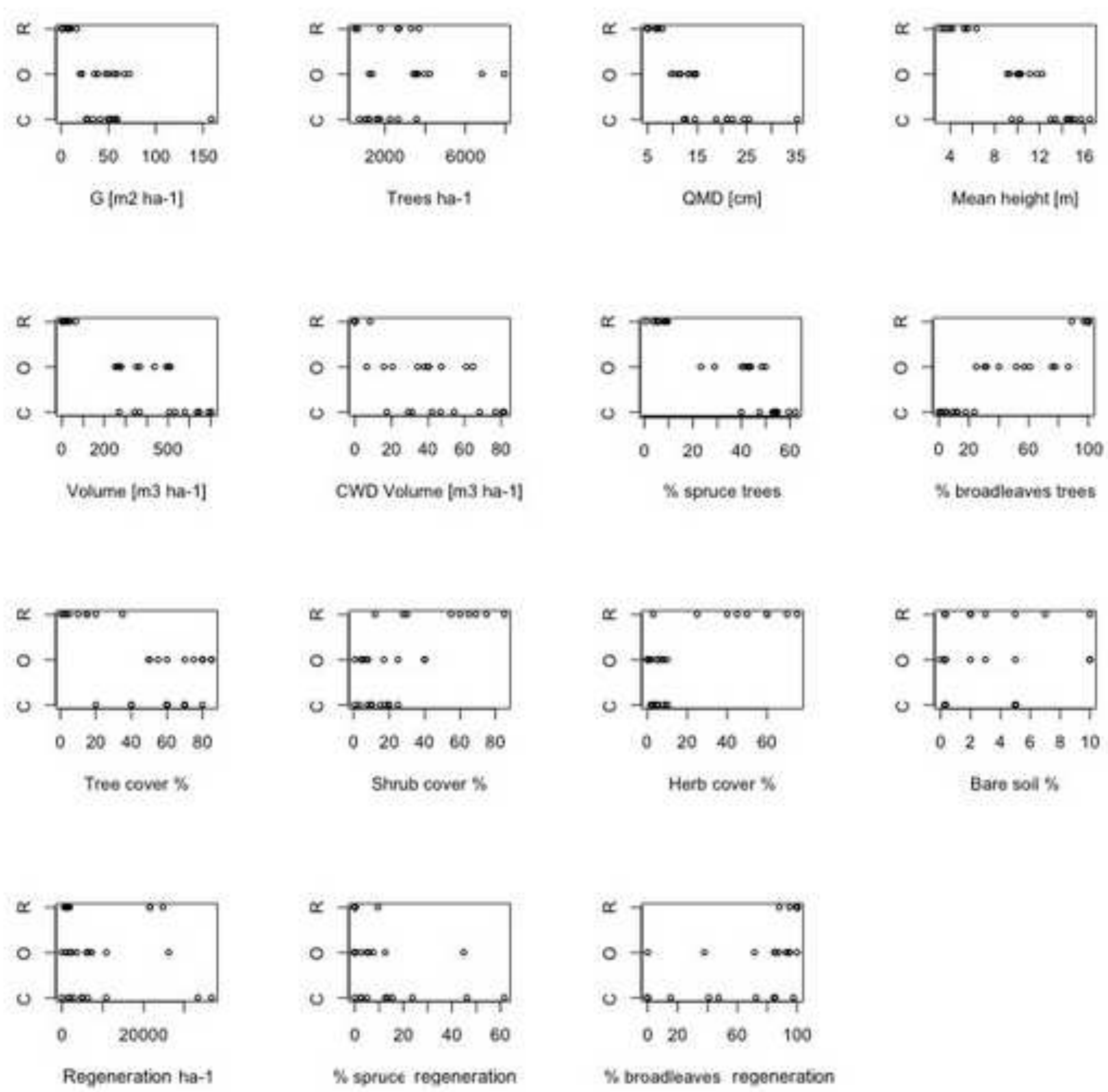

Figure 4
Click here to download high resolution image

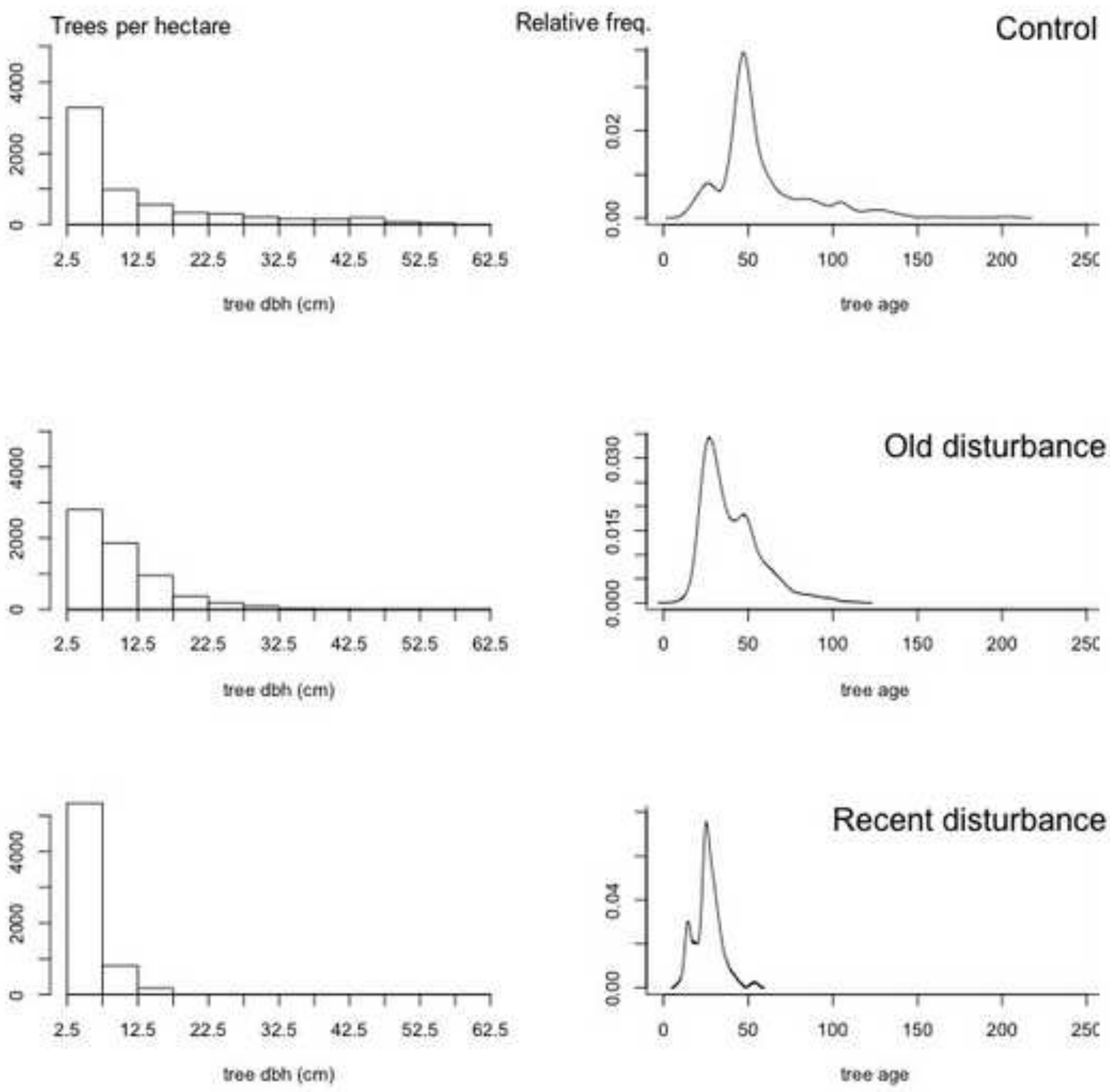

Figure 5
Click here to download high resolution image

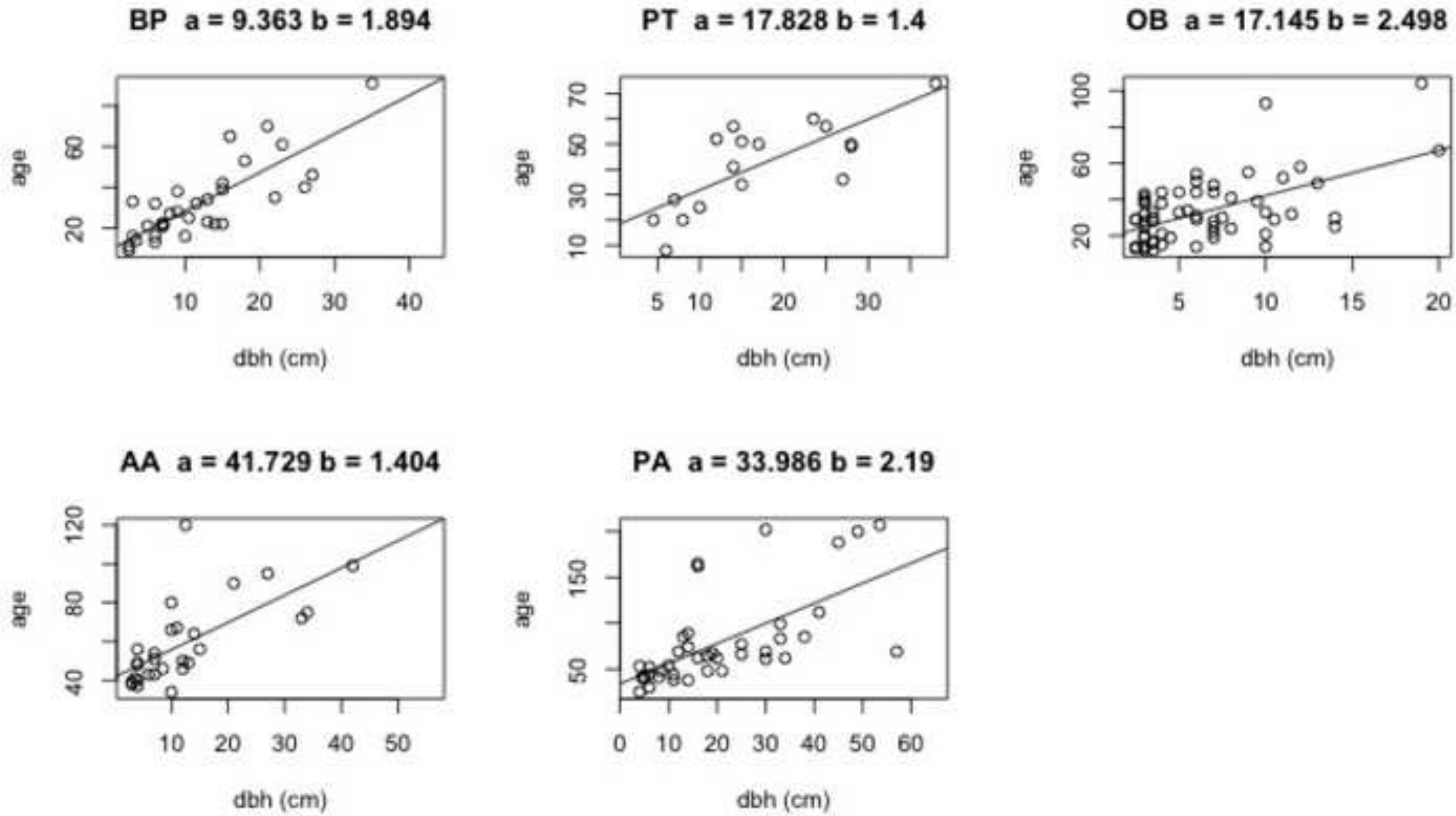

Figure 6
Click here to download high resolution image

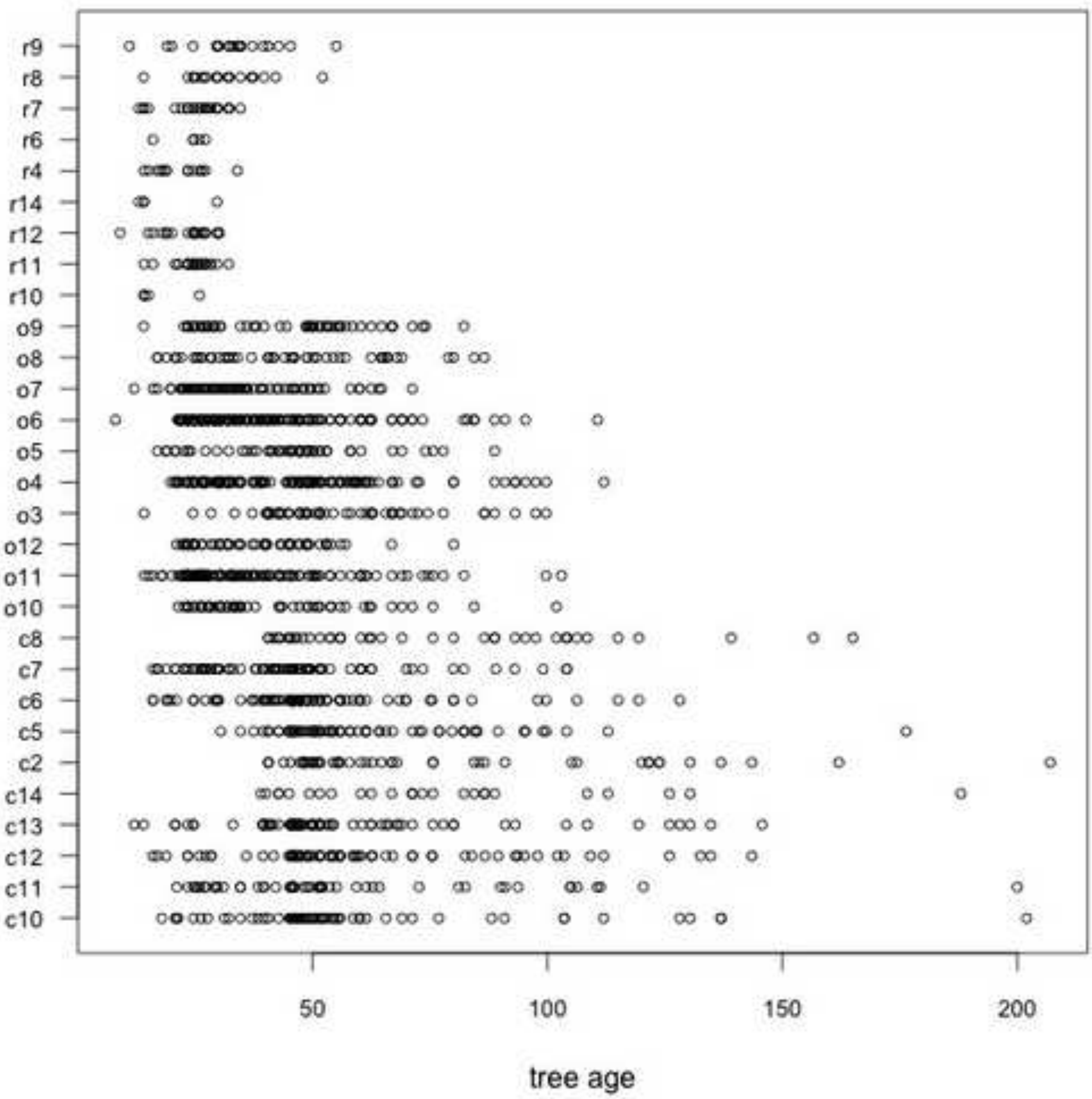

Figure 7
Click here to download high resolution image

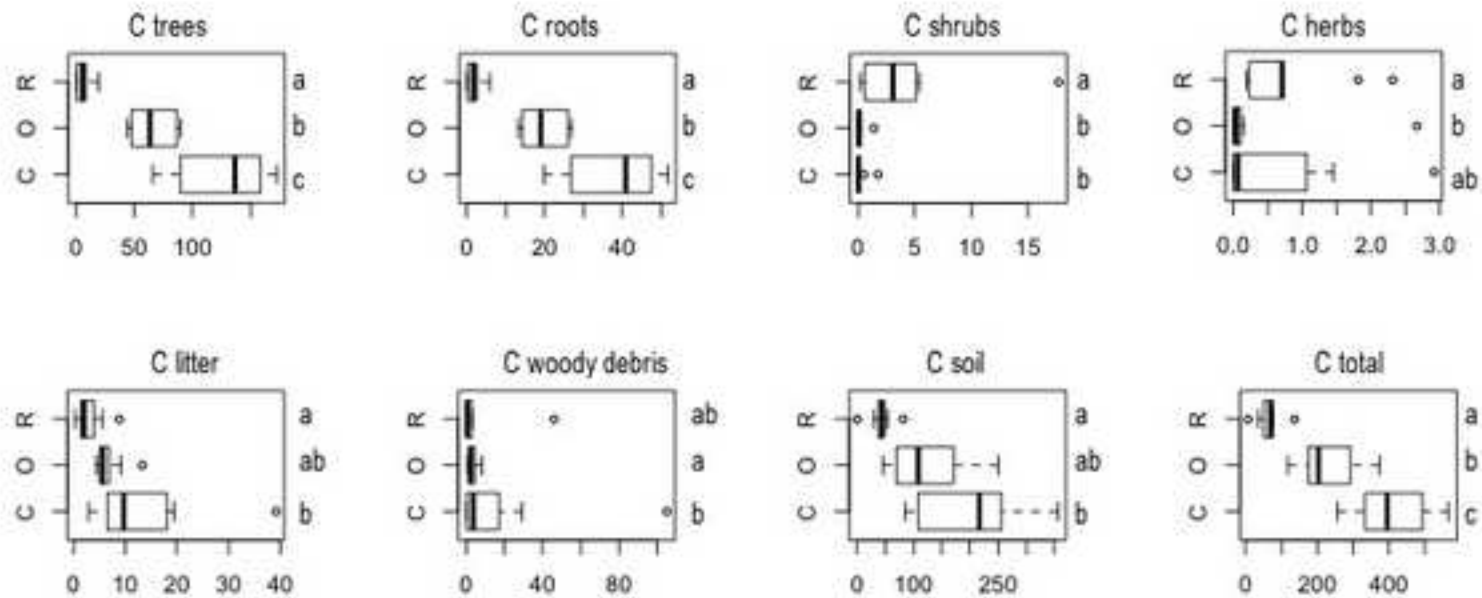

Figure 8a
Click here to download high resolution image

Figure 8b
Click here to download high resolution image

Figure 8c

[Click here to download high resolution image]

Supplementary Material

Click here to download Supplementary Material: s1.xlsx

KML File (for GoogleMaps)

Click here to download KML File (for GoogleMaps): pallesieux.kml