

Student thesis series INES nr 344

Comparing *Ips typographus* and *Dendroctonus ponderosus* Responses to Climate Change with the use of Phenology Models



Ida Pettersson

2015

Department of

Physical Geography and Ecosystem Science

Lund University

Sölvegatan 12



Ida Pettersson (2015). *Comparing Ips typographus and Dendroctonus ponderosus Responses to Climate Change with the use of Phenology Models.*

Bachelor degree thesis, 15 credits in *Physical geography and Ecosystem Analysis*

Department of Physical Geography and Ecosystem Science, Lund University

Level: Bachelor of Science (BSc)

Course duration: *March* 2015 until *June* 2015

Disclaimer

This document describes work undertaken as part of a program of study at the University of Lund. All views and opinions expressed herein remain the sole responsibility of the author, and do not necessarily represent those of the institute.

Comparing *Ips typographus* and *Dendroctonus ponderosus*
Responses to Climate Change with the use of Phenology
Models

Ida Pettersson

Bachelor thesis, 15 credits, in *Physical geography and Ecosystem Analysis*

Supervisor: Anna Maria Jönsson

Department of Physical Geography and Ecosystem Science, Lund University

Exam committee:

Cecilia Akselsson

Dan Metcalfe

Cover picture: *Ips typographus* galleries. Photo: Anna Marntell © Reprinted with permission.

Abstract

Bark beetles are a subfamily of insects living in and breeding on woody plants. Some of the bark beetle species have the ability to attack living trees, and thereby the potential to cause major forest damage. These forest damages can have a significant ecological and economic impact to forest ecosystems and foresters. In this study, phenology models were used to compare the responses to climate change of two species, the European *Ips typographus* and the North American *Dendroctonus ponderosa*, focusing on the beetles' voltinism. One existing model for *I. typographus* was used, and then adjusted to fit for the conditions demanded by *D. ponderosa*. In addition, it was evaluated how *D. ponderosa* could develop if the species was established in Sweden, and if it potentially could imply a threat to Swedish forests. The modeled results reveal that as a consequence of climate change, the potential geographic extent and phenology of bark beetles will be altered. By the end of the 21st century, bark beetles populations will have expanded further north and to higher altitudes, and their bivoltine potential will be increased. As a consequence, the outbreak potential might increase. According to climate conditions, *D. ponderosa* has the potential to establish in Europe. Due to its shorter generation time, *D. ponderosa* has a higher bivoltine potential than *I. typographus* in European conditions. However, the susceptibility of host plants also plays an important role for bark beetle establishment, and how much of a threat *D. ponderosa* could imply to Swedish forest ecosystems depends substantially on the vulnerability of the main Swedish tree species to *D. ponderosa* infestation. Regarding all bark beetles, appropriate forest management is vital to reduce the bark beetle outbreak risk.

Keywords: Bark beetles, Phenology models, Voltinism, Climate Change, *I. typographus*, *D. ponderosa*, forest damage.

Sammanfattning

Barkborrar är en grupp av insekter som lever av och i vedartade växter. Vissa av barkborrarna har förmågan att angripa levande träd, och därav kan de potentiellt orsaka storskaliga skogsskador. Dessa skogsskador kan ha en betydande ekologisk inverkan på skogars ekosystem samt betydande ekonomisk inverkan för skogsägare och samhällen som är beroende av skogsbruk. I den här studien användes fenologimodeller för att jämföra två barkborrarters respons till klimatförändringen. Arterna var den Europeiska *Ips typographus* (Granbarkborre) och den Nordamerikanska *Dendroctonus ponderosa* (Contortabastborre), och fokus låg på barkborrarnas voltinism, det vill säga hur många generationer som kan utvecklas under en säsong. För modelleringen användes en existerande modell för *I. typographus* som sedan modifierades för att anpassas till *D. ponderosa* levnadsförhållanden. Hotet som *D. ponderosa* eventuellt skulle kunna innebära för svenska skogar utvärderades också. De modellerade resultaten visar att till följd av klimatförändringen kommer barkborrarnas potentiella geografiska utbredning samt fenologi att ändras. Vid slutet av det här århundradet kommer barkborrepopulationerna att ha expanderat norrut samt till områden belägna på högre altituder. Potentialen till att utveckla två generationer per år kommer att ha ökat. Till följd av detta kan även risken för storskaliga utbrott av barkborrar öka. Enligt både nutida och framtida klimatförhållanden har *D. ponderosa* möjlighet att etablera sig i Europa. På grund av dess kortare utvecklingstid har *D. ponderosa* dessutom en större potential till att utveckla två generationer per år än *I. typographus* i Europa. Känsligheten hos värdräden spelar emellertid också en stor roll för barkborrars etablering, och hur stort hot *D. ponderosa* skulle kunna innebära för svenska skogar beror huvudsakligen på hur känsliga de viktigaste svenska trädarterna skulle vara för angrepp av *D. ponderosa*. Gällande alla barkborrearter är det ytterst viktigt att använda rätt skogsförvaltningsmetoder för att minska risken för nutida och framtida barkborreangrepp.

Nyckelord: Barkborrar, fenologimodellering, voltinism, klimatförändringar, *I. typographus*, *D. ponderosa*, skogsskador.

Acknowledgements

I would like to thank my supervisor Anna Maria Jönsson for her dedication in helping and supporting me through my thesis, with valuable comments and suggestions for improvements during the modeling and writing process. I would also like to thank friends and family for their support during the work, especially to my course mates for always being there with discussions and laughter during this course period.

Contents

1. Introduction	1
1.1. Aim	1
1.2 Limitations	2
2. Background.....	2
2.1 Climate change and its impact on insects	2
2.2 Bark beetles.....	3
2.3 <i>Ips typographus</i> and <i>Dendroctonus ponderosa</i>	4
2.4 <i>Ips typographus</i> outbreaks	6
2.5 <i>Dendroctonus ponderosa</i> outbreaks.....	7
2.6 Forest management aspect	7
3. Methods	8
3.1 Phenology models	8
3.2 Climate Data	8
3.3 Phenology models properties	9
3.3.1 <i>Ips typographus</i> model	9
3.3.2 <i>Dendroctonus ponderosa</i> model	10
3.4 Lower temperature threshold calculations	12
3.5 Model simulations and figure drawing	12
4. Results	13
4.1 Day of winter recovery and initiation of spring flight	13
4.2 Initiation of summer flight	15
4.3 Completed development of the first generation	18
4.4 Completed development of the second generation	18
4.5 Lower temperature thresholds.....	23
5. Discussion.....	24
5.1 Modeled <i>Ips typographus</i> phenology.....	24
5.2 Comparison with previous <i>Ips typographus</i> studies	24
5.3 Modeled <i>Dendroctonus ponderosa</i> phenology, and comparison between the species	25
5.4 The lower temperature thresholds aspect	26
5.5 Negative effect of climate change to bark beetles.....	27
5.6 Is <i>Dendroctonus ponderosa</i> a potential threat to Swedish forests?.....	27
5.7 The management aspect.....	28
5.8 Suggestions for improvements	29
6. Conclusion	29
7. References	30

1. Introduction

Conifers once green, now dying grey. A forest that used to flourish with birdsong, now remarkably quiet. Vast landscapes of trees without needles as long as the eye can see. That might be what encounters the one who enters a forest exposed to a large scale attack of bark beetles.

Bark beetles are a subfamily of insects, living in and breeding on woody plants. In the subfamily, some of the species possesses the ability to attack living trees. Due to this ability, bark beetles can have a significant ecological impact on forest ecosystems (Wood 1982). Furthermore, they might imply a large economic impact to forest owners and societies depending on forestry (Grégoire et al. 2015). Two of these species are the European *Ips typographus* and the North American *Dendroctonus ponderosa*. Following climate change, bark beetles phenology and population dynamics may change (Bentz and Jönsson 2015). Through temperature increase, the beetle's active season can be longer and change in their voltinism may support an increase in number of generations per year. Consequentially, bark beetles might imply an increased negative ecological and economic impact to forests ecosystem and forest owners in the future (Bentz and Jönsson 2015). However, if bark beetles response to climate change can be understood, then the potentially greater threat they will imply to forest ecosystems can be evaluated, and necessary measures needed to prevent attacks can be taken.

To reach an understanding about bark beetles response to climate change, models are useful tools. Modeling bark beetle response to climate change is a current research topic, and many studies have been performed on for example *I. typographus* and *D. ponderosa* (Bentz and Jönsson 2015). In this study, phenology models are used to compare *I. typographus* and *D. ponderosa*'s response to climate change. In addition, the potential threat *D. ponderosa* would imply to Swedish forest ecosystems is evaluated. Bark beetles are frequently spread over country borders by international trading and import (Grégoire et al. 2015) and today, the rate of introduction of new bark beetle species to Europe is accelerating (Kirkendall and Faccoli 2010). These alien species might imply a threat to forest ecosystems. Concerning Sweden, *D. ponderosa* could potentially be such a threat (Hall 2015). If so, knowledge about the threat *D. ponderosa* would imply is vital to be able to adapt measures needed to prevent a successful establishment.

1.1. Aim

The main aim of this study is to compare *I. typographus* and *D. ponderosa* responses to climate change with aid of phenology models, for a future climate scenario until the year 2090 in Europe.

Objectives:

1. To model *I. typographus* and *D. ponderosas* response to climate change considering their phenology and voltinism, with the following life cycle events included as model outputs for 30 year periods: day of winter recovery, initiation of spring flight, day of completed development of the first generation, initiation of summer flight and day of completed development of the second generation.

2. To model the percentage of days below the lower temperature threshold for survival for *I. typographus* and *D. ponderosa* for each 30-year period.
3. To compare *I. typographus* and *D. ponderosa* in terms of phenology and response to climate change.
4. To evaluate how *D. ponderosa* could develop if the species was established in Sweden. Would *D. ponderosa* imply a threat to Swedish forest ecosystems?

1.2 Limitations

This study focuses on bark beetle phenology, rather than the whole population dynamics. The dynamics and effects of outbreaks are only shortly discussed. Also the bark beetles potential to change the carbon balance of a forest ecosystem is only shortly mentioned and not further investigated in this study. Although the number of bark beetle species exceeds 6000, this study only includes two of them, chosen due to their high economic and ecologic impact on different continents. Even if this study focuses on bark beetle phenology, not all phonological aspects are evaluated. For example, even though it might be possible for the bark beetle to develop three generations per season in some parts of Europe, only the first and second generation is considered in the models used in this study. Also, development restrictions due too high temperatures are not considered. For example, temperature over 42-50°C usually inhibit the activity and development of the beetles and eventually kill them (Wood 1982). Finally, even though the association with bark symbiotic fungi is very important for some bark beetle species, it is not taken into great consideration in this study since it is a very complex association (Lindgren and Raffa 2013).

2. Background

Due to the current climate change, bark beetle population dynamics, voltinism and outbreak potential might be altered (Bentz and Jönsson 2015). In this section, some background information required to reach an understanding about this potential alteration is presented. The fundamental biological and phenological properties of bark beetles are presented, and an introduction to the species *I. typographus* and *D. ponderosa* is given.

2.1 Climate change and its impact on insects

As a consequence of anthropogenic emissions of greenhouse gases to the atmosphere, global climate change is occurring. During the time period 1901-2012, the global mean temperature increase was 0.89° C, and throughout the 21st century, it is expected to continue to increase with 1.5 to 4.5°C (IPCC 2014). This climate change is currently affecting earth's ecosystems, and will continue to do so. Insects are especially sensitive to altered living conditions by climate change. This is partly due to climate, and especially temperature, acting as direct mortality, growth rate and development control for the majority of insects, but also due to their short generation time (Bale et al. 2002). Herbivory insects can be affected by climate change directly or indirectly. Directly, when for example temperature increase affects their activities and physiology and

indirectly, when their living environment is altered by climate change, for example, if the state of their host plants is altered. For herbivory insects, changes in voltinism, development rate, geographical distribution and extent of host plant exploitation are some of the impacts of altered temperature. Consequentially, insect outbreaks are predicted to be dramatically affected by future temperatures increases (Bale et al. 2002).

2.2 Bark beetles

Bark beetles (Coleoptera: Curculionidae, Scolytinae) are a subfamily of insects living in and breeding on woody plants. They were described by Wood (1982) as a subfamily consisting of more than 6000 different species, which can be found wherever woody plants grow all over the world. The four life stages of bark beetles are egg, larvae, pupae, and adult (see *Figure 1*). The majority of their life time is spent as larvae. Bark beetles are dependent on their flight ability for swarming and movement between breeding trees and new host trees. Except for this movement, they spend most of their time inside the plants. Each species of bark beetles is most commonly adapted to breed in one or a few host species only. Furthermore, different species are adapted to live in different parts of the host plants, although the majority feed on the phloem, the innermost layer of the bark. Even though the majority of the bark beetles live in dead or dying plant tissue, for example recently harvested timber, some species also have the ability to settle in living, thriving plants and eventually kill them (Wood 1982). This small proportion of all species are called aggressive (Bentz et al. 2010) and they have the potential to cause major forest destruction and alter both the structure and species composition of forest ecosystems (Karvemo and Schroeder 2010). The mortality of the host tree is caused mainly by the excavating of tunnels in the plant tissue by larvae and adults (Bentz et al. 2010), but some species also have associations with fungi such as the blue-stain fungi which can be harmful and sometimes deadly to the host plants (Wermelinger 2004). Although only a small fraction of all bark beetle species can attack living trees, for example, less than 1 % of the hundreds of species found in western United states

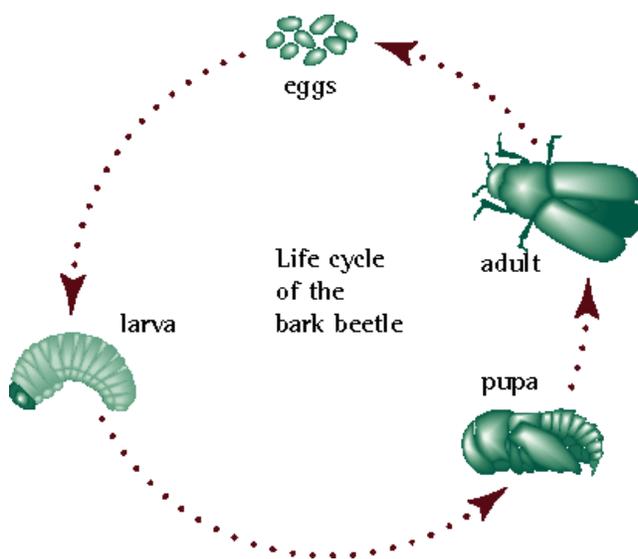


Figure 1: The life cycle of bark beetles. Source: British Columbia Ministry of Forests, Lands and Natural Resource Operations.

and Canada (Bentz et al. 2010), they are still one of the most important disturbance factors in forests. Bark beetles have the potential to cause major economic losses to forest owners (Karvemo and Schroeder 2010) since they can be the source of tree mortality at landscape-scale level (Bentz et al. 2010). Since many bark beetle traits such as development rate and cold hardening are temperature dependent, changes in climate can alter, sometimes drastically, bark beetle population dynamics and voltinism (Bentz and Jönsson 2015). The result can be either positive or negative for the populations. However, during the last decades, increased

forest damages caused by bark beetles have been observed, triggered by an increase in storm damage, but also in higher temperatures which have favored the species (Seidl et al. 2007). At the same time, since the bark beetles population dynamics are influenced by climate change through both direct effects like temperature, and indirect effects such as changes in host plants and associated fungi, their response to climate change is complex and future predictions cannot be done without uncertainties (Bentz et al. 2010). The extent of human measures taken to prevent attacks also greatly contributes to outbreak dynamics (Wermelinger 2004).



Figure 2: A coniferous forest in British Columbia where trees have turned red after being infested by the bark beetle *D. ponderosa*. Photo: British Columbia Ministry of Forests, Lands and Natural Resource Operations.

2.3 *Ips typographus* and *Dendroctonus ponderosa*

Two bark beetle species with high ecological and economic impact are *Ips typographus* (Spruce bark beetle) and *Dendroctonus ponderosa* (Mountain pine beetle). They are described by Karvemo and Schroeder (2010) as two species with both similarities and differences (see *Table 1*). *I. typographus* is mainly a European species; found substantially where its main host plant, *Picea abies* (Norway spruce), grows. It is distributed in most of the European countries, but can also be found in Japan, North Korea, South Korea, Algeria and others (Cognato 2015). *D. Ponderosa* is a North American species, found in southern British Columbia and portions of western Alberta in Canada and in most of the western United States (Bentz et al. 2010). Its primary host plant is *Pinus contorta* (Lodgepole pine), although it also has the ability to breed on other species such as *Pinus monticola* (Western white pine), *Pinus ponderosa* (Ponderosa pine) and *Pinus albicaulis* (White bark pine) (Karvemo and Schroeder 2010). There are also some differences regarding the species phenology. For example, while *I. typographus* enters diapause during the cold season, the winter survival of *D. ponderosa* is instead even more dependent on their cold hardening (Six and Bracewell 2015). Cold hardening is a process where the beetles

self-produced cryoprotectant compounds such as glucose prevents them from freezing (Bentz and Jönsson 2015). Larvae is the most common life stage for *D. ponderosa* overwintering, and it is also the most cold tolerant life stage (Six and Bracewell 2015). Also the voltinism differ between the two species. While *I. typographus* is univoltine or occasionally bivoltine, meaning that one or sometimes two generation is produced every year, *D. ponderosa* is mainly univoltine and occasionally semivoltine, meaning that one or sometimes only a half generations is produced every year (Bentz and Jönsson 2015).

Table 1: Comparison in latitudinal range, voltinism, winter survival method and size between *I. typographus* and *D. ponderosa*. Source: Karvemo and Schroeder (2010) and Bentz and Jönsson (2015).

	<i>Latitudinal range</i>	<i>Voltinism</i>	<i>Winter survival method</i>	<i>Size</i>
<i>I. typographus</i>	43° N to 66° N	Univoltine, bivoltine	Diapause and cold hardening	4.2-5.5 mm
<i>D. ponderosa</i>	31° N to 60° N	Semivoltine, Univoltine	Cold hardening	3.5-6.8 mm



Figure 3: Young *Ips typographus* beetles. Photo: James Keith Lindsey.



Figure 4: An adult *Dendroctonus ponderosa* beetle. Photo: British Columbia Ministry of Forests, Lands and Natural Resource Operations.

Regarding the two species interactions with their surrounding ecosystem, there are some differences. While *D. ponderosa* prefer healthy host trees, *I. typographus* breed on dead or dying trees primarily (Lindgren and Raffa 2013). However, when populations densities increases due to favored living conditions, also *I. typographus* have the ability to attack living trees and outbreaks may occur (Karvemo and Schroeder 2010). For *I. typographus*, the main outbreak trigger is storm felling events or other disturbances since they provide the beetles with an excess amount of breeding substrates (Marini et al. 2013). Consequentially, after tree felling storms, the abundance of *I. typographus* is higher in non-cleared forest areas, and the outbreaks often starts in windthrows (Wermelinger 2004). Outbreaks of *D. ponderosa* are not as dependent on disturbances since they are better adapted to breed on standing trees. In fact, they prefers standing trees over fallen and are rarely found in fallen ones (Six and Bracewell 2015). Both

species prefer large tree trunks over thin ones, and a tree diameter larger than 15 cm is required (Wermelinger 2004; Six and Bracewell 2015). For both species, the risk for outbreaks increases when the host plants susceptibility is increased by for example drought (Karvemo and Schroeder 2010). The main host tree species for *I. typographus* and *D. ponderosa*, *P. abies* and *P. contorta*, both possess some resistance against the beetles, but when “mass attack” occurs, that is, when a high density of beetles attack over a short period of time, the defense system will be overcome and the tree colonized (Jönsson et al. 2009; Powell and Bentz 2009). Outbreaks may cause enormous economic losses to forest owners (Karvemo and Schroeder 2010), which have happened for both the species. While outbreaks of *I. typographus* generally last for 3-6 years (Wermelinger 2004), outbreaks of *D. ponderosa* normally last around 10 years (Karvemo and Schroeder 2010).

2.4 *Ips typographus* outbreaks

In Europe, attacks by *I. typographus* have caused significant forest damage during several outbreaks. For example, two great storm events triggered bark beetle outbreaks during the end of the 20th century in central Europe: Vivian in February/March 1990 and Lothar in December 1999 (Wermelinger 2004). Lothar affected among other countries Switzerland, where 2,191,000m³ of wood was damaged by *I. typographus* following the storm between 1999 and 2009 (Grégoire et al. 2015). Sweden has also been affected by attacks, with three great outbreaks since 1960, whereof the first one was the most devastating (Karvemo and Schroeder 2010). Following the latest of them, the storm Gudrun in January 2005, 3,200,000m³ of wood was damaged by *I. typographus* (Skogsstyrelsen 2014). *I. typographus* will expectantly have an even higher ecological and economic impact in the future since the forest susceptibility to outbreaks is increasing with the increasing forest damage by storms observed in Europe (Marini et al. 2013).



Figure 5: A coniferous forest in Sweden where the trees have lost their needles after being infested by *I. typographus*. Photo: Anna Marntell © Reprinted with permission.

2.5 *Dendroctonus ponderosa* outbreaks

In western North America, outbreaks of *D. ponderosa* have caused several severe outbreaks, mainly restricted to British Columbia (Karvemo and Schroeder 2010). In British Columbia, *P. contorta* is one of the main commercial trees species, and up till the year 2012, 700 million m³ of *P. contorta* wood have fallen victim to *D. ponderosa* (Ministry of Forests 2012). Since 2000 and still going on, the biggest outbreak ever recorded takes place in British Columbia (Karvemo and Schroeder 2010). The outbreak has turned the forested area where it takes place from a small sink to a large source of carbon to the atmosphere (Kurz et al. 2008). In a comparison between *I. typographus* and *D. ponderosa* by Karvemo and Schroeder (2010), it was concluded that up till the year 2010, *D. ponderosa* had killed 60 times more forest, and it is described as a more aggressive species. Its high effectiveness in killing living trees in comparison to *I. typographus* depends on different factors. Firstly, *D. ponderosa* is better adapted than *I. typographus* to breed in living, standing trees. Secondly, it takes fewer individuals of *D. ponderosa* to overcome the defense system of a living tree. Finally, *D. ponderosa* have lower egg gallery densities than *I. typographus*, which favors the larvae's growth (Karvemo and Schroeder 2010).

2.6 Forest management aspect

Human forest management and trading activities can alter the outbreak potential and geographical distribution of bark beetles. Like many insects, bark beetles are frequently spread over country borders by international trading and import (Grégoire et al. 2015). When colonizing a new area, some species can become invasive. To forest ecosystems, invasive bark beetles can pose a major threat, and at the same time, there is acceleration in the rate of introduction of alien species to Europe (Kirkendall and Faccoli 2010). By the year 2010, there were 18 alien bark beetle species established in Europe, whereof two, *Grathotrichus materiarius* originating from eastern North America and *Xyleborinus attenuatus* originating from East Asia, could be found in Sweden. Concerning Sweden, it was stated in a report by Hall (2015) that alien species might potentially be easier established in the country in the future, if climate conditions develops in a for them favorable way. *D. ponderosa* is one of the species mentioned as a potential threat in the report (Hall 2015). Another important aspect of forest management is the choice of tree species for reforestation. In addition, high species diversity has proven to decrease a forest susceptibility to bark beetle attack (Grégoire et al. 2015). In many cases, exotic bark beetles have increased chances of successful establishment if their primary host plants are available. Concerning *D. ponderosa*, its major host plant, *P. contorta*, is not native I Sweden. However, it can still be found in Sweden since it has been planted by foresters. During the 1970's and 80's, *P. contorta* became more important for Swedish forestry due to its high productivity in comparison to the native *Pinus sylvestris*. Since restrictions against plantations of *P. contorta* were made in the 80's and 90's due to the species extensive infection of *Gremmeniella abietina* (fungus), the plantation decreased. However, the introduction of *P. contorta* to Swedish forests continues and only by the year 2001, 550 000 hectares had been plated in northern Sweden (Karlman 2001).

3. Methods

In this study, the comparison of *I. typographus* and *D. ponderosas* responses to climate change was accomplished by using two models: One existing model for *I. typographus*, and one *D. ponderosa* model which was developed starting from the *I. typographus* model. Data-sets with future climate scenarios were used as input for the models. The results were used to evaluate and compare the species response to climate change. The main focus lies on the beetles' voltinism, that is- how many generations of each species that can be developed during one year. Since bark beetle mortality due to cold temperatures during winter is not included the models, a separate model for calculations of the percentage of days below certain threshold values was also developed.

3.1 Phenology models

The models used to analyze *D. ponderosa* and *I. typographus* responses to climate change are phenology models. Phenology is the study of the timing of recurring biological events affected by seasonal climate changes (Tauber and Tauber 1976). Diapause is an example of such an event. When it comes to understanding insects dynamics and populations growth, phenology studies are indispensable (Tauber and Tauber 1976), and they can be used to display biological events at both spatial and temporal scales. Since bark beetles depend on both temperature and synchrony between different life stages and the seasons for their development, phenology models are useful tools for estimating their growth and outbreak potential (Bentz and Jönsson 2015) Except for development time, diapause and cold hardening are frequently occurring parts of phenology models. With aid of the phenology models, the spatial and temporal differences in bark beetle voltinism could be calculated.

3.2 Climate Data

An ensemble of two climate data-sets was used as input to the model. The climate sets each consist of a radiation scenario and a regional climate model. The radiation scenario used for both the sets is RCP 8.5. The RCP 8.5 scenario presupposes an increase in forced radiation of 8.5Wm^{-2} by the end of the 21st century in comparison to pre-industrial values (IPCC 2014). Amongst the RCP scenarios, RCP 8.5 is the one that presupposes the highest increase of forced radiation. The regional climate models used are IPSL-RCA4 and NorESMI-RCA4, which have both been dynamically downscaled from global climate models. These models are both derived from EURO-CORDEX. EURO-CORDEX is part of the international CORDEX initiative, which is sponsored by the World Climate Research Program (WCRP) and endeavors to improve the quality of climate change predictions for all land regions of the world (Euro-Cordex). An ensemble was used since it gives an overview of the spread amongst different climate models. The phenology models were run twice, once with each climate data-set, and then the average of the two climate data-sets was used for the model outputs. The two regional climate data-sets used, IPSL-RCA4 and NorESMI-RCA4, were chosen amongst the available climate models from EURO-CORDEX. These two ensemble members were chosen since they represents different parts of the variation amongst the climate models, and therefore also represent the main

variation of a larger ensemble: all climate models available through EURO-CORDEX (Wilcke 2015). The climate data cover Europe, have a spatial resolution of $0.4^{\circ} \times 0.4^{\circ}$, approximately $50 \times 50 \text{ km}$, and comprise information about predicted daily min, max and mean temperatures at 2m height above the surface. They are bias adjusted. A latitude/longitude mat- file covering Europe and Northern is also included. It also possesses the spatial resolution of $0.4^{\circ} \times 0.4^{\circ}$.

3.3 Phenology models properties

The models used in this study utilize gridded daily mean and max temperature data as input. With aid of the models, the variables day of winter recovery (A), initiation of spring flight (B), day of completed development of first generation for early and late individuals (C), initiation of summer flight for early and late individuals (D) and day of completed development second generation for early and late individuals (E) were calculated for each $50 \times 50 \text{ km}$ grid cell. All variables were calculated for the 30-year time periods 1971-2000, 2001-2030, 2031-2060 and 2061-2090 (Figure 6).

3.3.1 Ips typographus model

The *I. typographus* model was developed by Jönsson et al. (2007), and has been used in published studies (Jönsson et al. 2007; Jönsson et al. 2009; Jönsson et al. 2011). As input for the model, information about mean and max temperatures from the climate scenarios was used. Variables A-E were calculated according to the following:

- A. The day of winter recovery is the end of winter hibernation and start of the spring. It is modeled to take place after 120 degree days (dd). Degree days is an expression of the thermal sum of a number of days over a development threshold. For *I. typographus*, the development threshold for all life stages (egg, pupae, larvae and adult beetle) is 5°C .
- B. At the initiation of spring flight, the swarming starts. Conditions for *I. typographus* swarming to start are emergence of winter hibernation and a daily max temperature of 20°C . However, daily max temperatures simulated from the climate scenarios used in this study tend to be approximately 4°C lower than temperature records measured in the field during March to August (Jönsson et al. 2011). That can be explained by the structure of the grid cells: maximum temperature values represent the average of a $50 \times 50 \text{ km}$ area, which makes the grid cell values lower than the maximum temperatures from point measurements. Therefore, the daily max temperature has been modified to 16°C in this model.
- C. The development time from eggs to adult beetles is measured in degree days (dd). The development time differs between individuals in sun exposed locations (early) versus shaded locations (late). At sun exposed locations, the development time is 625 dd, whereas 750 dd are required for shaded locations. The development starts 7 days after the initiation of spring swarming. That is the time needed to reinsure that about 50 % of the oviposition has taken place.

- D. The flight for the first generation (summer flight) starts at the first day when/ if daily max temperature exceeds 20°C and diapause has not yet been initiated. Initiation of diapause is in turn dependent on daily mean temperature and on a day length threshold. If the daily mean temperature is below 15°C, swarming cannot occur. The limit of 15°C for daily mean temperatures is set to avoid improperly calculations of summer flight on unusually warm autumn days. The day length threshold was calculated separately according to another model, and then put into the *I. typographus* model.
- E. The development time for the second generation in dd is the same for those of the first generation, 625 dd and 750 dd for early and late individuals, respectively. The development starts 7 days after the initiation of summer swarming.

3.3.2 *Dendroctonus ponderosa* model

The *D. ponderosa* model was developed starting from the *I. typographus* model. Some of the thermal and developmental thresholds of the *I. typographus* model were adjusted to fit for the conditions of *D. ponderosa*. Also for this model, information about mean and max temperatures from the climate data-sets was used. Variables A-E were calculated according to the following:

- A. The day of winter recovery is assumed to be the same as for *I. typographus*, 120 dd. It is a reasonable assumption due to the species similarity in size and in other thermal thresholds.
- B. The thermal threshold for *D. ponderosa* to initiate flying, and thereby swarming, varies between 19.44 and 20.0°C (McCambridge 1971), which is almost the same as for *I. typographus*. Therefore, the same temperature limit for initiation of flight, 16°C, was used for *D. ponderosa*.
- C. The thermal threshold for development is slightly higher for *D. ponderosa* than for *I. typographus*, 5.6°C (Safranyik and Wilson, 2006). However, the development time from egg to adult beetle is shorter. According to Safranyik and Wilson (2006), the development time is 478.3 dd at a constant temperature of 18°C and 546.6 at 27°C. These dd values were used in the model to represent development in sunny versus shaded conditions. The temperature difference in between 18°C and 27°C, 9°C, is reasonable to represent an approximate difference between such locations.
In a study by Amman (1972), factors affecting the oviposition of *D. ponderosa* was examined. In this study, eggs were counted 10-13 days after mating. According to this, it is reasonable that about 50 % of the eggs can have been laid after 7 days also for *D. ponderosa*. Therefore, the same time from between initiation of spring swarming and start of the development of the first generations, 7 days, was used for the *D. ponderosa* model.
- D. The flight of the first generation (summer flight) starts at the first day when daily max temperature exceeds 20°C if the daily mean temperature is not yet below 5.6°C, which is the lower development threshold for *D. ponderosa*. No considerations needed to be taken in regards to reproductive diapause, since that is not part of *D. ponderosa*'s lifecycle.

E. The development time for the second generation in dd is the same for those of the first generation, 478.3 dd and 546.6 dd for early and late individuals, respectively. Also here, the development starts 7 days after the initiation of summer swarming.

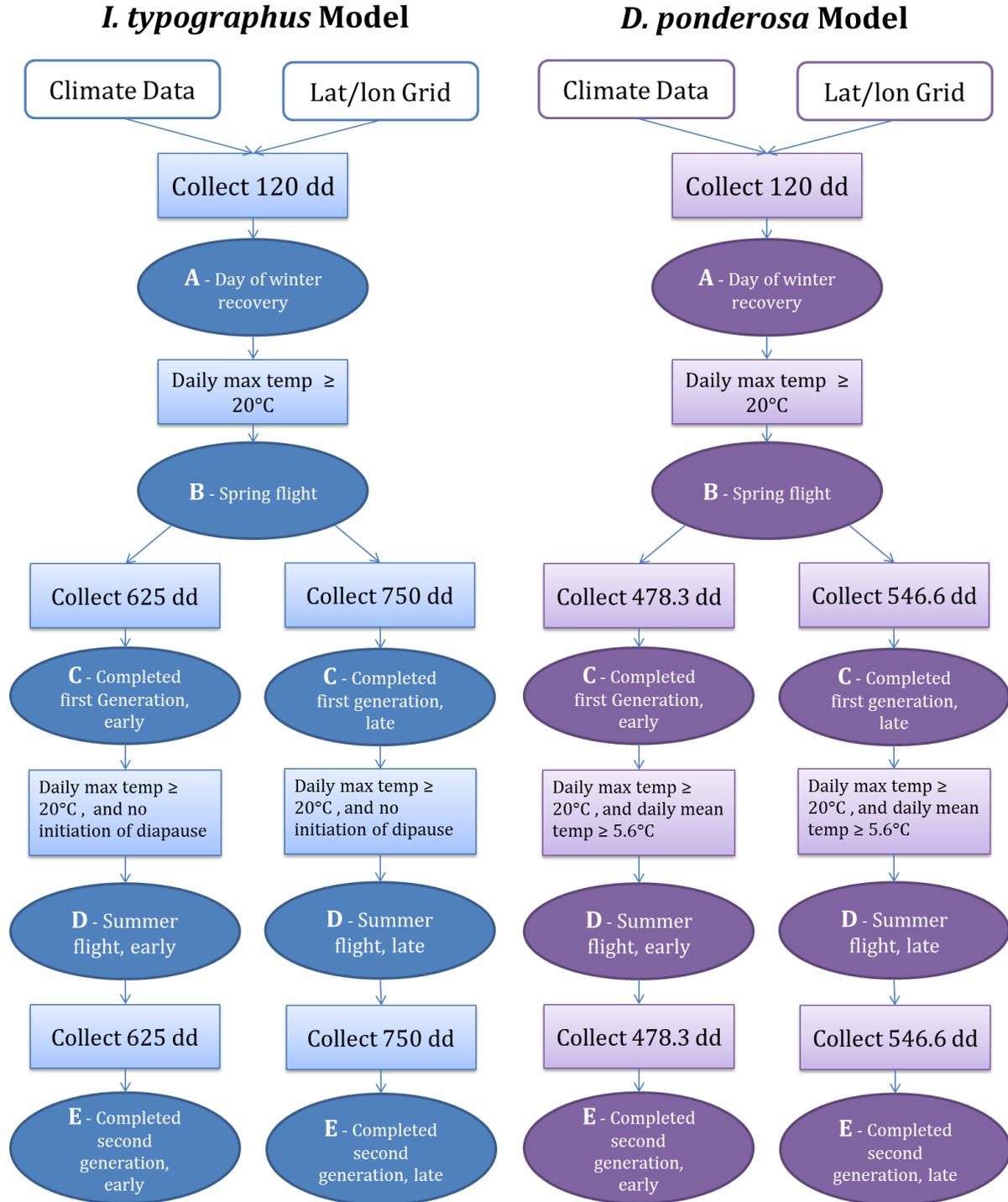


Figure 6: Schematic figure of the models used in this study. Abbreviation: dd = degree days. 5°C and 5.6°C are the thermal thresholds for development for *I. typographus* and *D. ponderosa*, respectively.

3.4 Lower temperature threshold calculations

One aspect of the bark beetles life cycles not included in the models is the potential mortality due to freezing caused by cold temperatures throughout the winter. If a certain temperature threshold is reached, the bark beetles dies and cannot continue their development the next year. The threshold values differ amongst the species and also amongst the different life stages of each species. For *I. typographus*, larvae are the least cold tolerant life stage and the mortality of the larvae is 100% when temperature reaches -12°C (Annala 1969). Regarding *I. typographus*, winter mortality mainly affect larvae and young adults and frequently only adult survive the winter (Faccoli 2002). *D. ponderosa* is more cold tolerant than *I. typographus*. Egg and pupae are the least cold tolerant life stages of the species, followed by adults and 1st, 2nd and 3rd instar larvae (Safranyik and Wilson 2006). The mortality of *D. ponderosa* eggs is 100% when temperature reaches -18°C , while pupae die between -18 and -34°C (Safranyik and Wilson 2006). For the lower temperature calculations, the temperature thresholds -12°C and -18°C were chosen to look further into. A model was developed to calculate the percentage of all days with a temperature that falls below -12°C or -18°C . For the model, information about min temperatures from the climate scenarios was used as input. The calculations were performed for each 30 year time period.

3.5 Model simulations and figure drawing

The phenology model scripts and the lower temperature threshold script were written and run in Matlab R2015a (Version 8.5). They created output in mat-files for all the variables needed (day of winter recovery, initiation of spring flight, day of completed development of the first generation for early and late individuals, initiation of summer flight for early and late individuals and day of completed development of the second generation for early and late individuals and percentage of days with a min temperature under certain thresholds). Using Matlab, figures were drawn to visualize the results for each 30-year time period. The figures displaying the results from the phenology models were designed to contain two subplots: One showing the timing of each event, meaning the day when it occurs, and the other showing the frequency of each event, meaning how often it will occur. The figures showing the results from the modeling of lower temperature threshold were designed to display frequency only.

4. Results

The results from this study reveals that according to the used models, the geographic area where development of one or two complete bark beetle generations is possible will expand northwards during the 21st century for both *I. typographus* and *D. ponderosa*. The day of winter recovery, initiation of spring flight and initiation of summer flight will happen at more locations and/or earlier by the end of this century compared to today. *D. ponderosa* develops faster than *I. typographus* and therefore possesses the potential to develop more generations per year for each time period. At the same time, the percentage of days with temperatures below the mortality threshold for each species will decrease during the 21st century.

4.1 Day of winter recovery and initiation of spring flight

For each time period, both the day of winter recovery and the initiation of spring flight occurs at the same time for *I. typographus* and *D. ponderosa* (see *Figure 7*), but the timing of the events varies throughout the time periods. With a warmer climate, the amount of degree days needed to initiate recovery from winter hibernation and spring flight can be accumulated faster and earlier in the year. Therefore, both day of winter recovery and initiation of spring flight take place slightly earlier for each 30 year time period. Between 1971 and 2000, winter recovery occurs around day 125, in the beginning of May, in the southern Scandinavia and Russia. In the major parts of central and southern Europe, it takes place earlier, and in the northernmost parts of Europe and the mountainous regions of Sweden and Norway, winter recovery doesn't occur until July or August. That is too late for the first generation to reach maturity the same year, at least for *I. typographus* who has got a longer development time. Since the winter mortality is high in these areas, and few *I. typographus* larvae survive the winter, most of these *I. typographus* individuals will not reach maternity at all. The situation is different for *D. ponderosa* since it is common for *D. ponderosa* individuals to hibernate as larvae and continued their development the following year. By the years 2061-2090, winter recovery will take place in May at many of the most northern locations, and even earlier in southern Scandinavia. Also in central and southern Europe, it will happen earlier than today. The initiation of spring flight always occurs shortly after the winter recovery. The accumulated degree days are not enough to initiate flight at all on some of the mountain tops of the Alps and on the Scandinavian mountains in the beginning of the time series. By the end of the 21st century, flight will occur also at those locations even though this flight might not result in mature individuals the same year or at all.

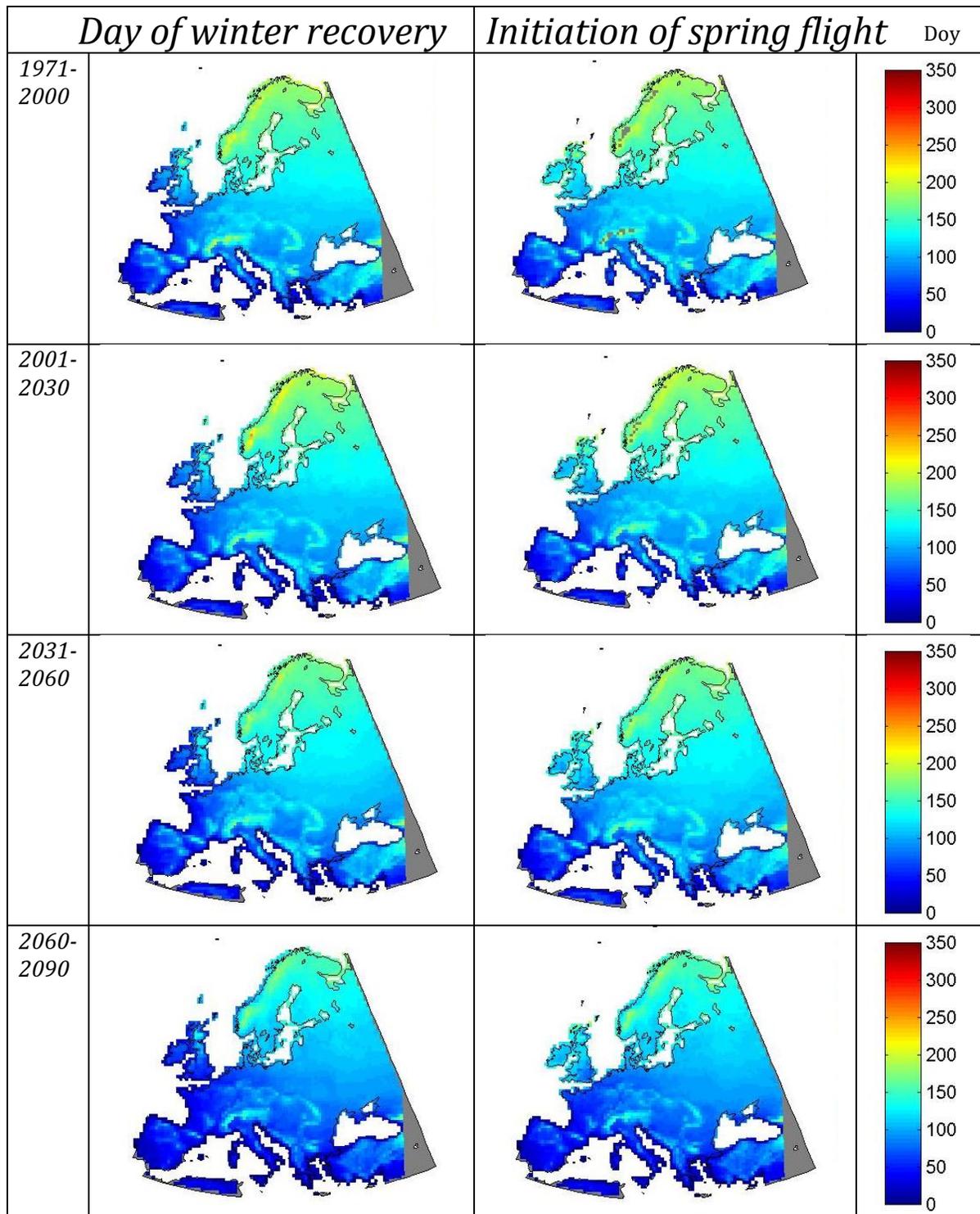


Figure 7: The timing of winter recovery and initiation of spring flight for *I. typographus* and *D. ponderosa*. Day of the year (Doy) and corresponding dates: 1st of April: 91, May: 121, June: 152, July: 182, August: 213, September: 244.

4.2 Initiation of summer flight

Initiation of the second generation, the summer flight, takes place when and if the first generation is fully developed, if diapause has not yet been initiated. For each modeled time period, the initiation of summer flight happens at more locations and starts earlier for the first individuals and later for the last individuals (see *Figures 8-9*). The early individuals swarm at the first possible day of swarming, and the late ones on the last possible day final. According to the model, initiation of summer flight did not occur in Sweden, Norway or Finland by the years 1971-2000. In central and southern Europe, summer flight did occur and was timed to start mainly between June and August and stop by day September and November. Already by the time period 2001-2030, summer flight occurs also in southern Sweden and Finland, and the geographical limits for where the event occurs continues to move northwards during the following time periods. First day of initiation of summer flight takes place earlier and last day takes place later for each location and time period. By the years 2061-2090, summer flight will occur in southern Sweden and many other parts of Scandinavia, starting in July and ending in September. When comparing *I. typographus* and *D. ponderosas* modeled timing of summer flight, it is evident that the flight can occur both earlier in the spring and later in the autumn for *D. ponderosa*. In fact, summer flight occurs at approximately the same geographic extent for *D. ponderosa* in 1971-2000 than for *I. typographus* in 1961-2090, and even earlier for *D. ponderosa*.

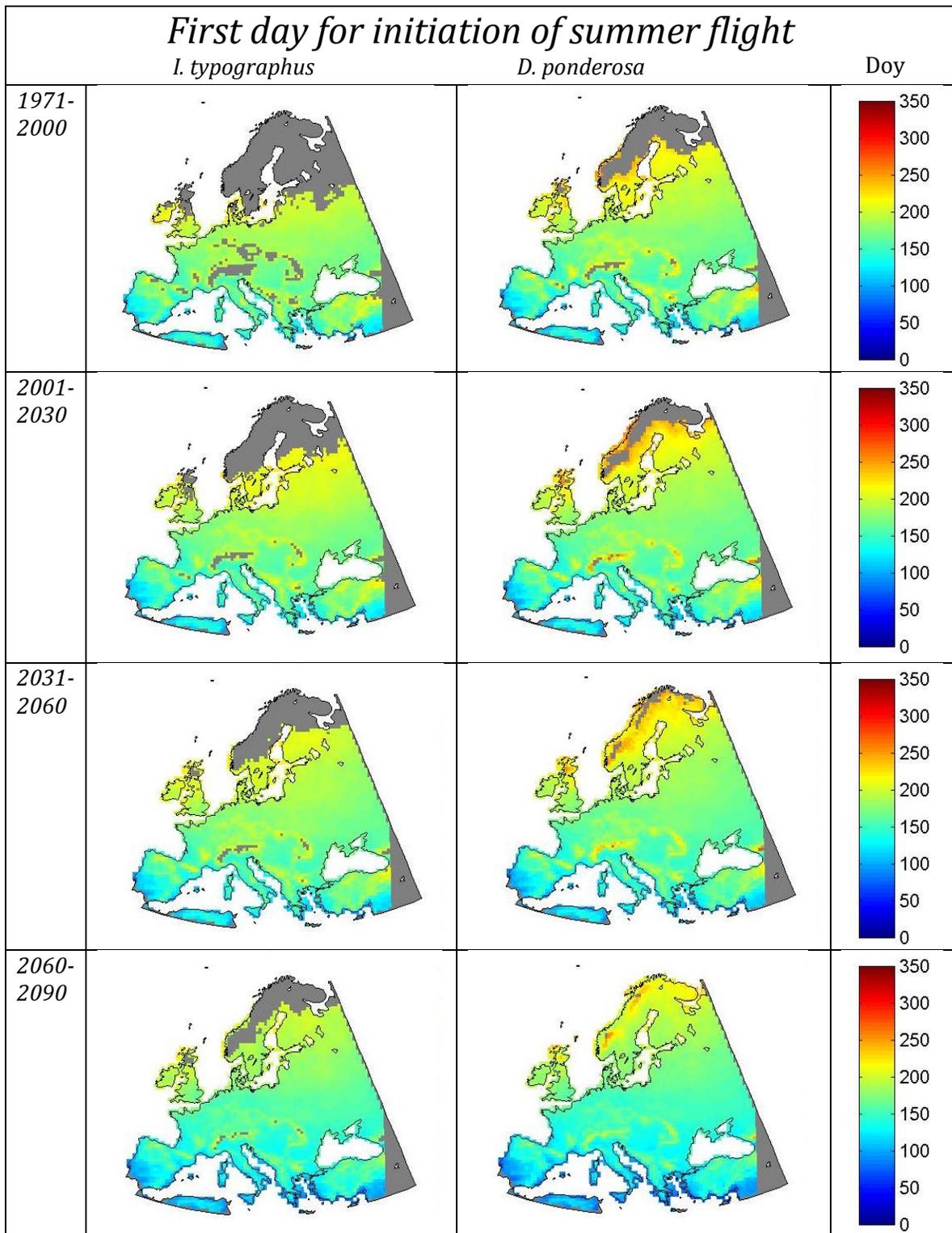


Figure 8: Timing of the first day of initiation of summer flight for *I. typographus* and *D. ponderosa*. Day of the year (Doy) and corresponding dates: 1st of April: 91, May: 121, June: 152, July: 182, August: 213, September: 244, October: 274. November: 305.

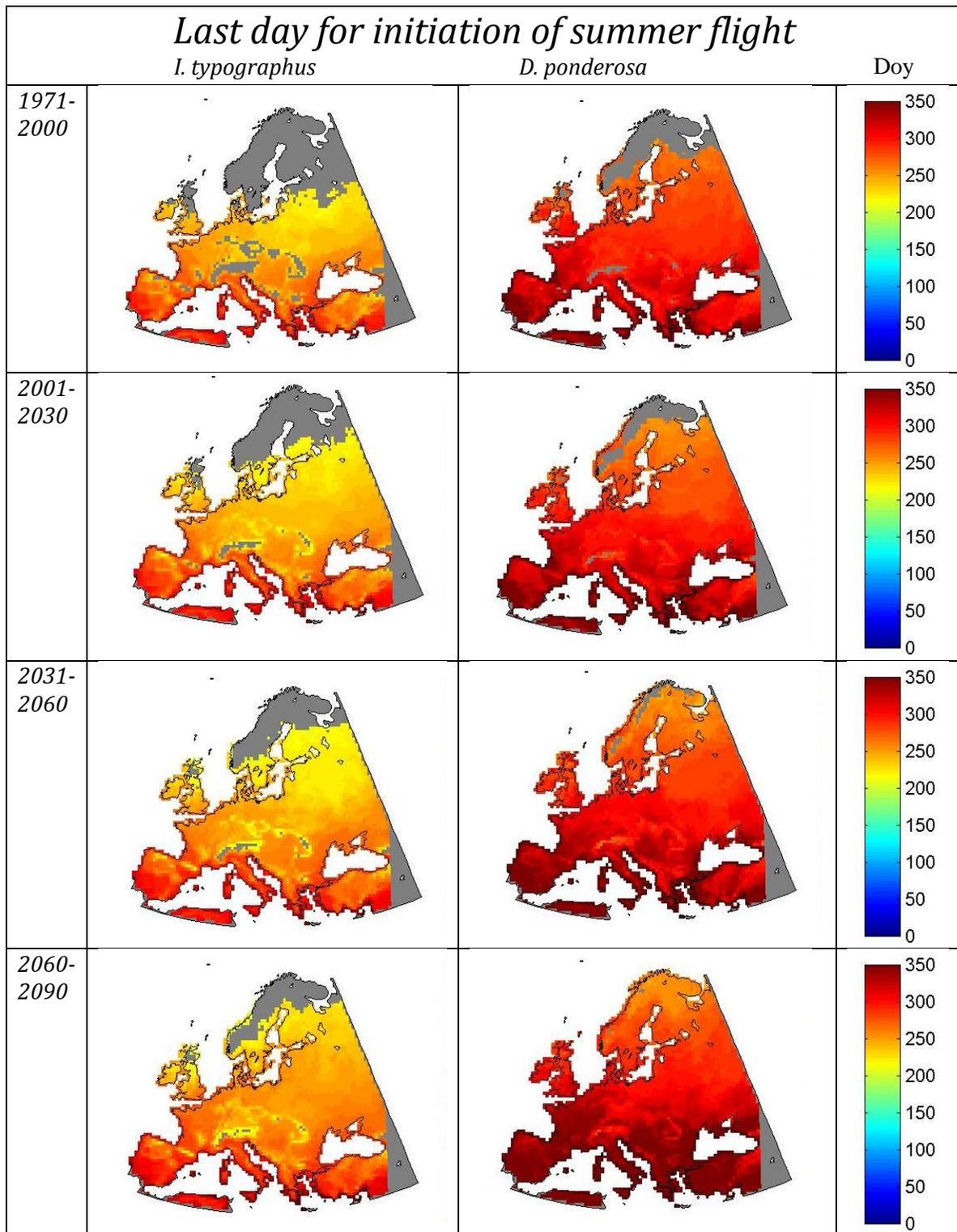


Figure 9: Timing of the last day of initiation of summer flight for *I. typographus* and *D. ponderosa*. Day of the year (Doy) and corresponding dates: 1st of April: 91, May: 121, June: 152, July: 182, August: 213, September: 244, October: 274. November: 305.

4.3 Completed development of the first generation

For each time period, the development of the first generation of beetles can be completed at a larger geographic area for both *I. typographus* and *D. ponderosa* according to the model (see *Figure 10*). Regarding *I. typographus* during 1971-2000, the development of the first generation was completed in 100% of the years in all parts of Europe except the major parts of Norway, northern Sweden and Finland as well as in some parts of the Alps. In 2001-2030, the area where generations are completed in 100% of the years has increased, and it continues to do so with time. During 2069-2090, the first generation of *I. typographus* is fully developed in all areas except in a small part of the Scandinavian mountains. For *D. ponderosa*, completion of first generation occurs slightly more often in all time periods compared to *I. typographus*. Regarding the late individuals, a somewhat lower fraction of all years leads to a completed development of the first generation for all time periods compared to the early individuals (*Figure 11*).

4.4 Completed development of the second generation

The total geographic area where completion of the development of a second generation is possibly will increase significantly during the 21st century for early and late individuals of both *I. typographus* and *D. ponderosa* (*Figure 12* and *13*). Concerning *I. typographus*, a complete development of a second generation was possible in many parts of Europe already by 1971-2000 according to the model. When looking at Sweden specifically, complete development of a second generation was not possible at all during 1971-2000. During 2001-2030, it is partly possible in southern Sweden, mainly for the early individuals. In 2031-2060, the fraction of completed generations continues to increase and by 2061-2090, complement of the second generations is possible in 100% of the years in the most southern parts of Sweden, even for the late individuals. Regarding southern and central Europe, complement of the second generations is possible almost everywhere in 2061-2090. Concerning *D. ponderosa*, completed development of a second generation is always possible in a larger area compared to *I. typographus*. For example, completion in 100% of the years was possible already 1971-2000 in the most southern part of Sweden, although only in a small area. By the end of this century, completion of a second generation of *D. ponderosa* will be possible in some areas where it will not be possible for *I. typographus*, for example in southern Finland and in some parts of the British islands.

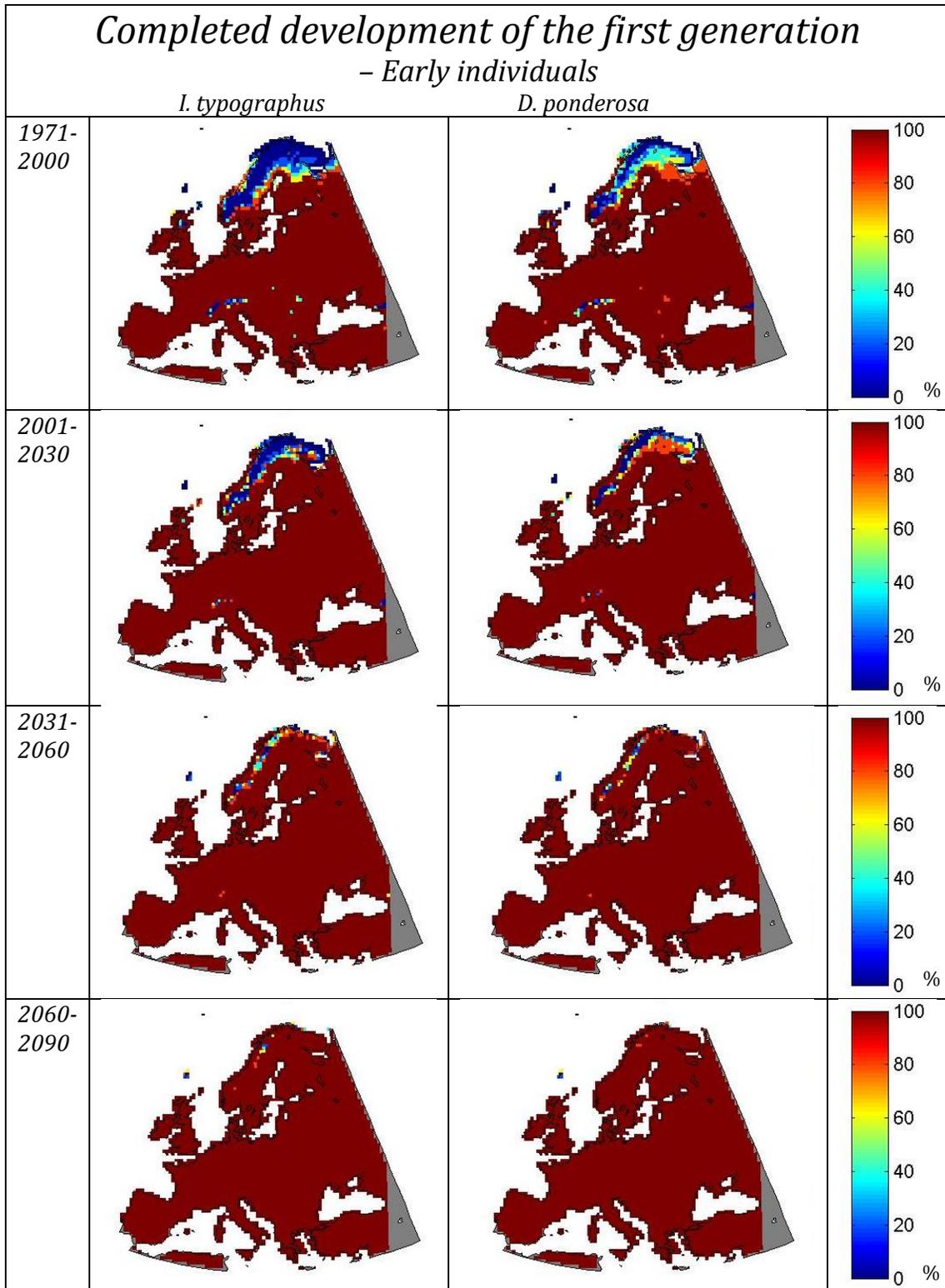


Figure 10: Percentage of completed development of the first generation of *I. typographus* and *D. ponderosa* beetles for early individuals.

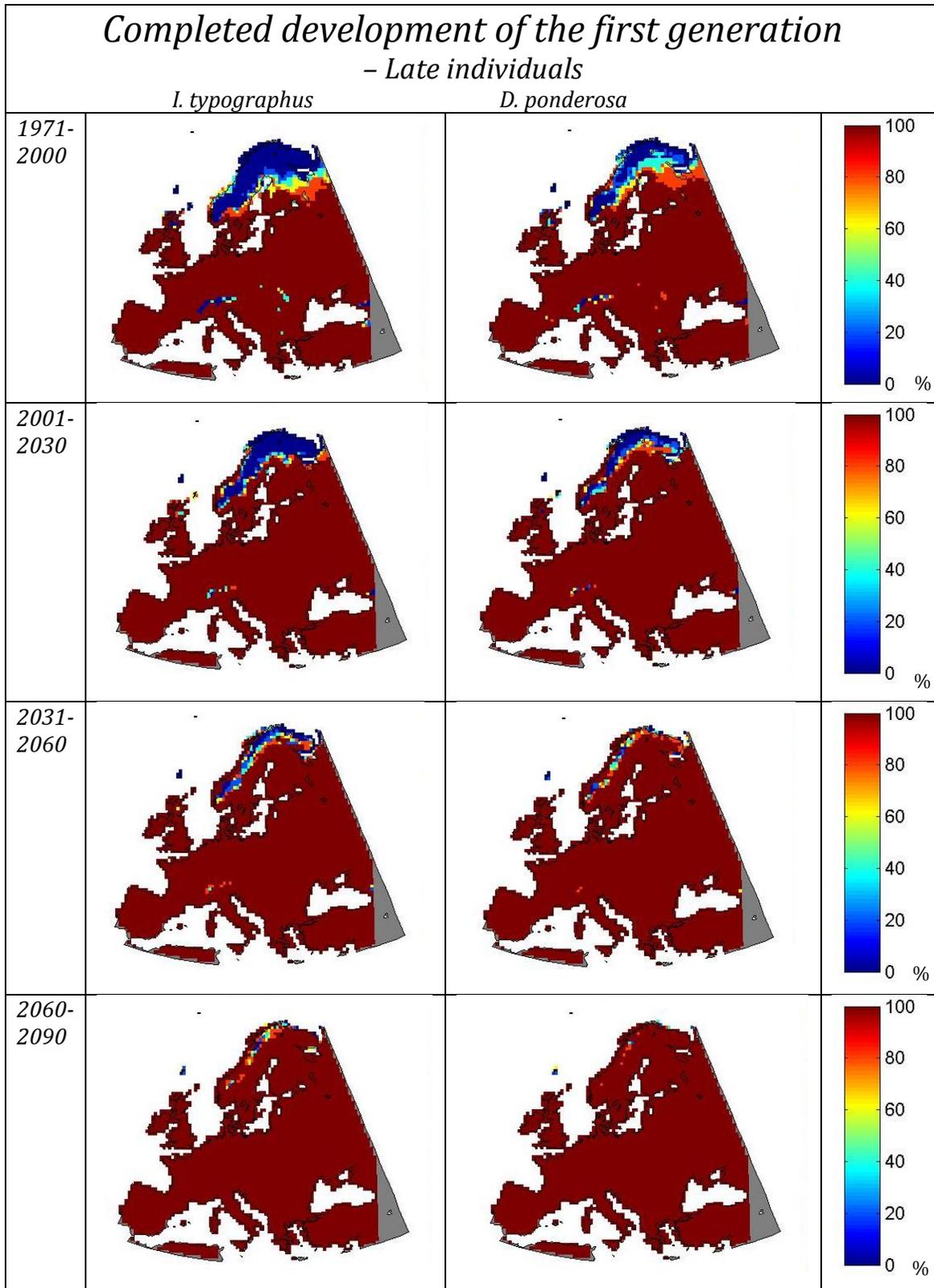


Figure 11: Percentage of completed development of the first generation of *I. typographus* and *D. ponderosa* beetles for late individuals.

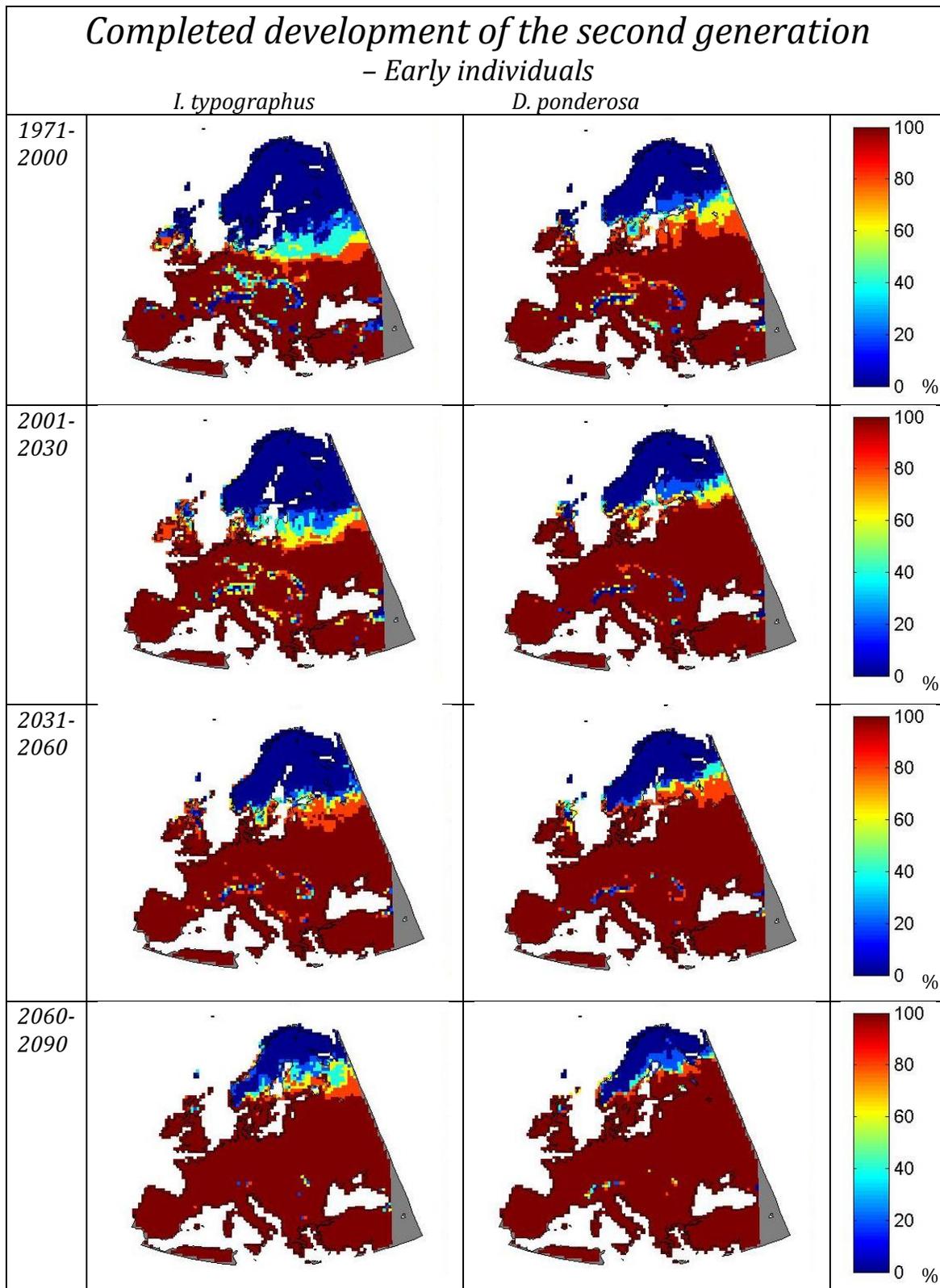


Figure 12: Percentage of completed development of the second generation of *I. typographus* and *D. ponderosa* beetles for early individuals.

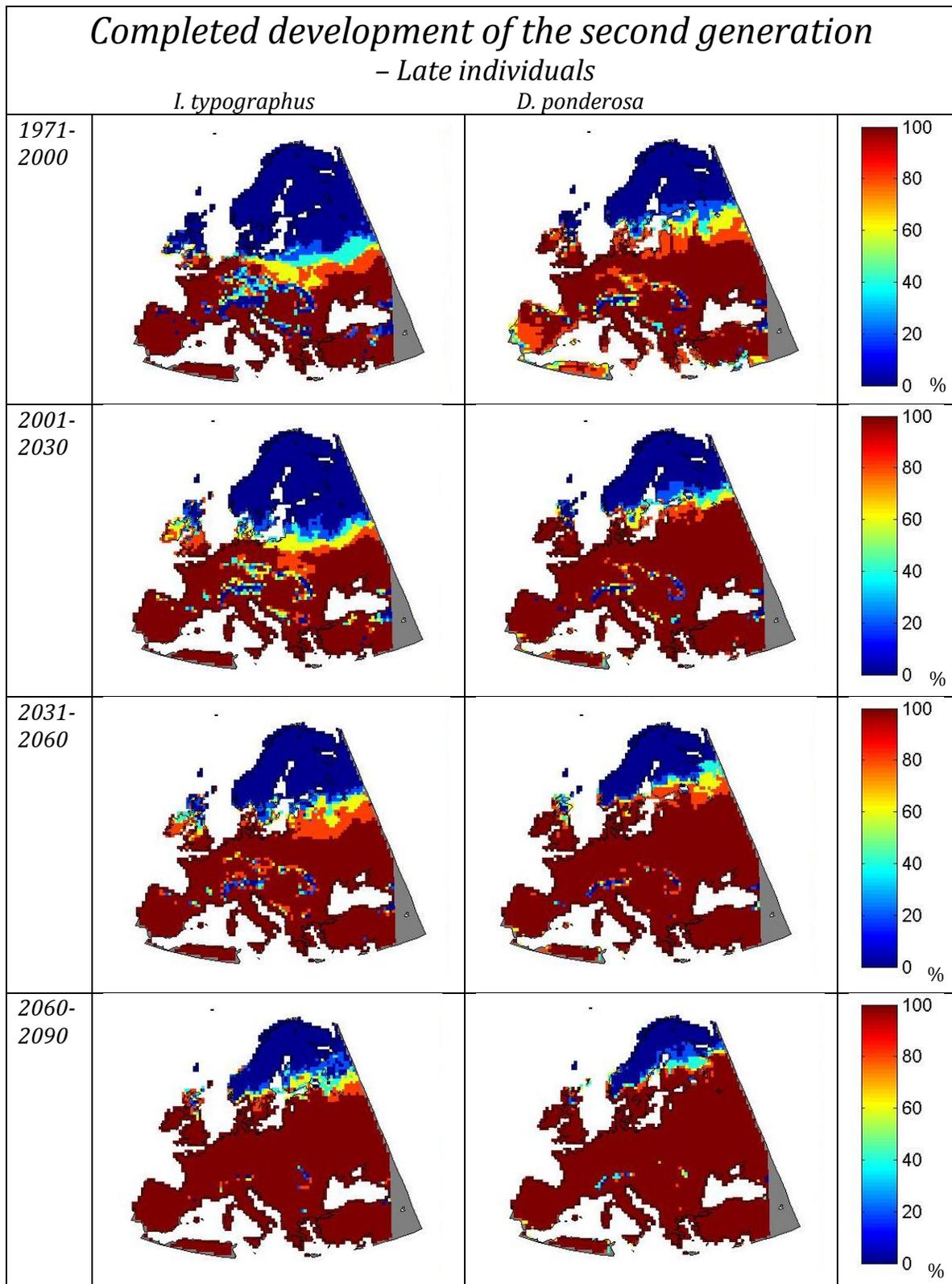


Figure 13: Percentage of completed development of the second generation of *I. typographus* and *D. ponderosa* beetles for late individuals.

4.5 Lower temperature thresholds

The number of days below the lower temperature limit for survival will decrease during the 21st century (Figure 14). For *I. typographus*, the lower mortality temperature for the most cold sensitive life stage, larvae, is -12°C. The corresponding temperature for *D. ponderosa*, for which the most cold sensitive life stage is egg, is -18°C. According to the model, the percentage of days with a min temperature at -12° or below was 0 in large parts of Europe already by 1971-2000. However, during this time period, large parts of northern Europe experienced many days with temperatures below -12°C. In southern Scandinavia and a large part of Eastern Europe, the amount of these cold days range between 5 and 10%. Further north, in northern Scandinavia and Russia, the percentage of days with a min temperature below -12° is even higher and reaches almost 35% as highest in an area close to Barents Sea. Going forward in time, a significant decrease in number of days with min temperature below -12°C is evident. By 2061-2090, the area where temperature never reaches -12°C has increased any also covers for example southern Sweden, Denmark and Norway. Nevertheless, the amount of cold days is still about 10% in some parts of the Scandinavian mountains and slightly higher in the most northern parts of Scandinavia and Russia. The percentage of days with a min temperature below -18°C is logically lower than those below -12°C. The model shows that in 1971-2000, the percentage of days with a min temperature below -18°C reaches a maximum of approximately 20% in a small area close to Barents Sea. Further south, in southern Scandinavia, it varies between 0 and 10 % of all days. By the end of this century, the percentage of days with a min temperature below -18°C will not exceed 5% in Europe, except at only a very small northern area.

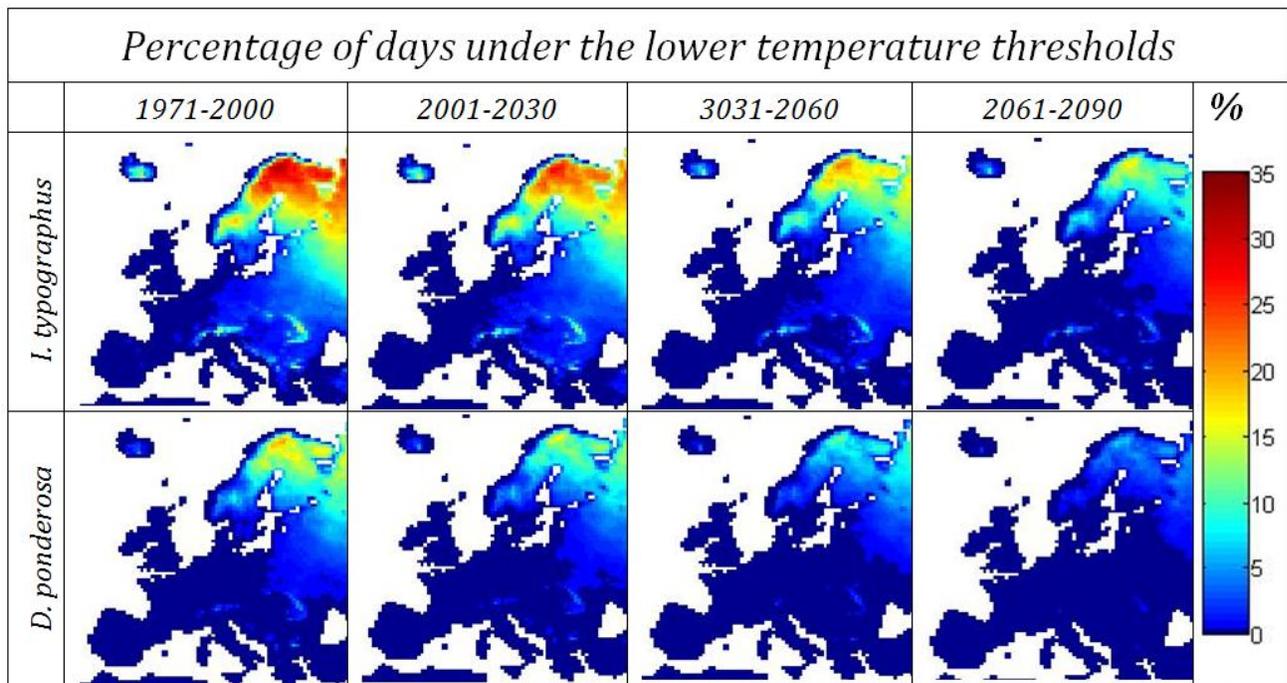


Figure 14: Percentage of all days under lower temperature mortality threshold (-12°C for *I. typographus* and -18°C for *D. ponderosa*).

5. Discussion

The modeling of *I. typographus* and *D. ponderosa* phenology clearly displays how the potential number of completed generations in Europe will increase with a warmer climate. Due to climate change, the geographical areas where completion of a first and second generation can occur will increase for both the species. The day of winter recovery and initiation of spring flight will be brought forward through the time periods. Winter recovery will for example happen about one month earlier in southern Sweden in 2061-2090 compared to 1971-2000. According to climate conditions, there is a risk of establishment of a *D. ponderosa* population with the potential to cause forest damage in Sweden if it was accidentally brought here. However, in addition to climate, there are other aspects such as availability of host plants that need to be considered as well.

5.1 Modeled *Ips typographus* phenology

Due to climate change, the geographical area where completion of a first generation of *I. typographus* can occur will increase and by the end of the 21st century include almost whole Europe. Also the area where completion of a second generation is possible will increase and by the end of this century include areas such as the majority of the British islands, southern Scandinavia and the Baltic states. However, one must keep in mind that in this study, *I. typographus* is modeled to have the possibility to live in locations where they do not have the possibility to establish in reality due to the lack of suitable host trees. That is the case for example in major parts of the Mediterranean area. When looking at Sweden especially, one can see that completion of the first generations of *I. typographus* was not possible in a relatively large part of the northern areas 1971-2000, but completion will not be possible in only a very small part of the country, in the most mountainous areas, by the years 2061-2090. While a completed development of a second generation of *I. typographus* was not possible in Sweden 1971-2000, it will be possible in the southern part of the country by the end of this century. With this higher bivoltine potential, the risk of outbreaks might increase.

5.2 Comparison with previous *Ips typographus* studies

The results from this study are similar to those found by Jönsson et al. (2009), who also modeled future bark beetle phenology response to climate change. They started with the same model as the one used in this study, but utilized other climate data as input, three climate data-sets from the Rossby Centre Regional Climate Model RCA3. The results from their study, which considers Sweden, also indicates earlier spring swarming and a greater possibility for summer swarming by the end of this century compared to today. Furthermore, Jönsson et al. found that by the end of this century, completion of a second generation will be possible in 63-81%, 16-33% and 1-6% of the years in south, mid and north Sweden, respectively (Jönsson et al. 2009). Those results are similar to the results from the investigation presented in this thesis. Another study on *I. typographus* life cycle response to climate change was performed by Lange et al. (2006). Lange et al. investigated the bivoltine potential among *I. typographus* in a changing climate in Norway using another phenology model. As input, they used both historical climate data from the

Norwegian Meteorological Institute and three different climate scenarios form two different models, focusing on the time periods 1961-1990 and 2071-2100. The results from their study indicate a higher potential for development of a second generation compared to results from this study. That is both for previous time and the future, even when they use the mildest scenario in terms of temperature increase (Hadley AGCM model with the B2 emission scenario). Lange et al. firstly looked at the period 1961-1990 and found a potential for bivoltinism along the Oslofjord. According to the study presented in this thesis, the bivoltine potential was 0 around the Oslofjord even slightly later, in 1971-2000. This study also suggests the bivoltine potential to be lower in Southern Norway by the end of the 21st century compared to the results by Lange et al, who's bivoltine potential reaches 100% further up in the mountainous areas. There are two major reasons for these differences in result between the studies. Firstly, the fact that Lange et al do not account for diapause, and consequentially, their bivoltine potential will always be higher compared to studies who do take diapause into account. Secondly, the climate data has been handled differently. In this study, the climate data was dynamically downscaled from global to regional climate model. Lange et al. on the other hand downscaled their climate data statistically. Statistical downscaling can lead to a higher spatial variability than dynamical downscaling, and that is the case here. The results by Lange et al. are more spatially detailed than the result from this study and one can assume them to be more accurate since empirical observations have confirmed the occurrence of a completed second generation along the Oslofjord in 1961-1990. This demonstrates how scale and downscaling methods is of great importance to consider in the modeling process. When looking at a limited geographical area with large differences in altitude, like Norway, a statistical downscaling is to prefer, while a dynamical downscaling method can work just as well when looking at a larger area, like Europe.

5.3 Modeled *Dendroctonus ponderosa* phenology, and comparison between the species

The modeling reveals that based on climate conditions, it would be possible for *D. ponderosa* to establish and successfully complete its life cycle in Europe. The geographic extent for the area where development of a complete first and second generation could be completed increases throughout the time periods. In comparison to *I. typographus*, *D. ponderosa* has the potential to develop faster and thereby complete more generations per year. That is due to the lower demand of accumulated degree days to complete development from egg to adult beetle. Therefore, *D. ponderosa* also has the potential to expand further north and to higher altitudes than *I. typographus*. When comparing the two bark beetle species, the most distinctive difference in their life cycles is that while *I. typographus* enters diapause during the winter, *D. ponderosa* does not. However, the species also have many similarities. For example, the temperature threshold for flight is the same for both species, 20°C. The oviposition of each species demands approximately the same amount of time. In addition, the minimum temperature threshold for development is similar, 5°C for *I. typographus* and 5.6°C for *D. ponderosa*. However, according to Wermelinger (2004), the minimum temperature threshold for development for *I. typographus* varies between 6 and 8.3°C, which is slightly higher than the 5°C used in this *I. typographus*

model. If this threshold value would be used in the model instead of 5°C, the development of *I. typographus* would consequentially start later and the differences in timing and percentage of completed first and second generations between the two species would be even greater. Since the species have many similarities regarding temperature thresholds and the focus of this study lies on the beetle's voltinism, this modeling method, where an existing *I. typographus* model was used to develop a model for *D. ponderosa*, is working well. The *D. ponderosa* model could be developed with only small adjustment from the original model. This simple method could most certainly be used also to investigate other bark beetle species phenology and voltinism. However, if the models should be developed to cover more of the population dynamics, they would need to look more different due to the fact that *I. typographus* enters diapause while *D. ponderosa* does not.

5.4 The lower temperature thresholds aspect

The models used in this study are good tools for calculating future bark beetle phenology in general, and especially for calculations of the potential of completed first and second generation. However, the models have their limitations since they do not take all aspect of the species life cycles into account. If one is interested in not only the uni- and bivoltine potential, but rather the future potential development of the entire bark beetle population, some more aspects of the bark beetle life cycles needs to be taken into account. Most importantly, how the population is affected by winter and with what individuals the spring starts. The models used in this study presuppose development to start from the beginning in the spring, with adult beetles waking up and straight away initiate a new generation. But also individuals from other life stages, such as different larvae, wake up and continue their development in the spring. This is especially important to consider for *D. ponderosa*, which does not enter winter hibernation and therefore in simplistic terms can continue to develop during the cold season as long as the temperature not goes under the development threshold of 5.6°C. *D. ponderosa* frequently hibernate as larvae. Another important aspect to consider is the beetle mortality by freezing due to cold temperatures. If a beetle population experiences an increase in number of generations developed per summer season, but in the same time experiences death due to cold temperatures during the winter season, the population might not increase in number of individuals in the long run. That may reduce the risks of large scale beetle outbreaks. Winter mortality due to freezing is potentially an important determinant for population growth regarding for example *I. typographus*, from which mainly adults survive the winter (Faccoli 2002). However, in the future, the percentage of days with a minimum temperature bellows the beetle species respective mortality limits will decrease following climate change. The temperature thresholds are -12°C and -18°C for *I. typographus* and *D. ponderosa*, respectively. Since the threshold temperature is higher for *I. typographus*, more *I. typographus* individuals are expected to die during the winter. Consequentially, the risk for a considerable reduction in number of individuals in the population during wintertime is higher for *I. typographus*. The risk will continue to be higher for *I. typographus* throughout the 21st century. Since the percentage of days under the temperature mortality limits decreases during the 21st century, winter mortality will be a less important part of *I. typographus* and *D.*

ponderosa population dynamics in the future. Also, the temperature thresholds mentioned here only applies to the most cold sensitive life stages of each beetle species. Not all individuals of any of the species will die when these temperatures are reached. For example, individuals of the most cold tolerant life stage of *D. ponderosa*, the third instar larvae, might survive temperatures down to -40°C (Safranyik and Wilson 2006). Furthermore, it should be considered that the model used to calculate the percentage of cold days is a large scale model which does not display the actual temperature for each specific location. For bark beetles, the temperature of highest importance is the one in the tree phloem or in forest litter where some beetles spend their hibernation. Due to insolation and radiation effects, the temperature at those protected sites can differ a lot from the air temperature (Faccoli 2002), which might increase the beetles' chance of winter survival. The chance of survival further increases if the beetles also are sheltered by a protective snow cover (Annala 1969).

5.5 Negative effect of climate change to bark beetles

Even though bark beetles in many cases will be strongly favored by climate change, they will not necessarily always be positively affected. One aspect that could be altered in a non-favorable way is the bark beetles development rate. The development rate of many bark beetle species has namely evolved to aid the beetle populations maintain suitable life cycle timing (Bentz et al. 2010). This implies to for example diapause and winter survival. In cold regions, many bark beetle species have evolved to make sure the population spend the winter in their least cold sensitive life stage. If development accelerates due to climate change, it might make the population spend their winter in a more cold sensitive life stage. That could in turn affect the population negatively by increased winter mortality due to freezing. Another aspect of climate change that could potentially affect bark beetles negatively is the host plants tissues humidity. Following climate change, conditions can be drier, and that might affect bark beetles positively or negatively. Positively, if the host plants susceptibility is increased in a way that favors the beetles. And negatively, if the humidity levels of the host plants host tissue gets too low to support the bark beetles development (Wood 1982). To further deepen the analysis of *I. typographus* and *D. ponderosa* responses to climate change, it would be useful to evaluate the potential of negative effects of climate change to the species populations.

5.6 Is *Dendroctonus ponderosa* a potential threat to Swedish forests?

Like other bark beetle species, *D. ponderosa* is occasionally moved into new areas by human activities such as trading of wood and exotic plant species (Six and Bracewell 2015). It allows us to raise the issue of the potential consequences of a *D. ponderosa* introduction to Sweden. Could *D. ponderosa* potentially imply a threat to Swedish forest ecosystem? The modeling performed in this study reveals that according to climate conditions, the North American *D. ponderosa* could potentially be established in Sweden. Due to its short development time, it could even develop faster and produce more generations per year than the native *I. typographus*. However, climate is not the only factor determining if a species will be successfully established at a new location or not. The interaction with the new ecosystem is of great importance, for example the

availability of suitable host plants. The main host plant of *D. ponderosa*, *P. contorta*, is not native in Sweden, although it can still be found there to a limited extent. Today, approximately 2 % of the Swedish forests have been reforested with *P. contorta* (0.55 of the 28 million hectares) (Karlman 2001; SLU 2015). *D. ponderosa* also have the possibility to breed on different tree species such as *P. monticola*, *P. ponderosa* and *P. albicaulis* (Karvemo and Schroeder 2010). Furthermore, *D. ponderosa* has proven to be able to adapt to novel host tree species. For example, while expanding eastwards in North America, *D. ponderosa* has successfully started to breed on *Pinus banksiana* (Jack Pine)(Cullingham et al. 2011). In this process of geographical expansion and adaptation to a new host species, *D. ponderosa* has showed no loss of genetic variability. This indicates that the species evolutionary potential to adapt had not been affected negatively by founder effects (Samarasekera et al. 2012). This potential to successfully establish a new population starting with very few individuals would facilitate a potential *D. ponderosa* establishment at new areas, such as Sweden. However, to get a deeper understanding about the potential threat *D. ponderosa* could imply to Swedish forests, an investigation of the susceptibility of *P. sylvestris* and *P. abies* to attacks by *D. ponderosa* is required. *P. sylvestris* and *P. abies* are the two major Swedish forest tree species, each accounting for about 40 % of the Swedish timber volume (SLU 2015). As earlier mentioned, *D. ponderosa* is a more aggressive species than the native *I. typographus*, and therefore it takes fewer individuals of *D. ponderosa* to overcome a trees defense system compares to *I. typographus* (Karvemo and Schroeder 2010). *D. ponderosa* is also better adapted to breed in living trees. Therefore, if *D. ponderosa* could successfully breed in *P. sylvestris* and *P. abies*, it might imply a significant threat to Swedish forest ecosystems. However, potential outbreaks are not likely to be as devastating as the ones recently noticed in British Columbia, since in comparison to Canada, Sweden has no overmature stands, which decreases the outbreak risk (Karvemo and Schroeder 2010). Overmature stands are stands that are reaching the end of their natural life span and whose health are consequentially declining.

5.7 The management aspect

Concerning both *I. typographus* and *D. ponderosa*, consideration of forest management is vital to prevent future large scale outbreaks. That will be especially important due to the increasing future bivoltine potential of both the species, which may increase the risks of outbreaks. However, if the forest susceptibility to bark beetle infestation can be reduced, the risk of outbreaks can be decreased considerably. Forests susceptibility can be decreased by making the forest more diverse regarding tree species composition, age and ground vegetation (Wood 1982). Another preventing measure would be to make the forest less sensible to windthrows. That can in many cases also be accomplished by making the forest more diverse (Wood 1982). If trees are overturned by storms, they need to be removed from the forest before bark beetles have gotten the chance to infest them in order to prevent potentially damageable population increases. Another challenge to be faced is the movement of bark beetle species by international trading and import. Today, there is an International standard for Phytosanitary measures (ISPM 15), instituted by the Integrated Pollution Prevention and Control (IPPC) in 2009. According to this

standard, traded wood needs to be either heat treated or fumigated with methyl bromide. In addition, it has to be debarked (Grégoire et al. 2015) However, since this standard is not enough to ensure bark beetle free importations, additional measures need to be instituted to reduce the rate of introduction of exotic bark beetles around the world. Regarding Sweden, considerations need to be taken about both the native *I. typographus* and possible future exotic species such as *D. ponderosa* to ensure a sustainable forestry. For example, the potential risk of *D. ponderosa* infestation should be considered when reforesting areas with *P. contorta*.

5.8 Suggestions for improvements

When adapting the *I. typographus* model to fit for *D. ponderosa*, some of the parameter values used were set to be the same for both the species due to lack of corresponding information. This include day of winter recovery and time between swarming and oviposition. Even though it seems justified to use the same values in these two cases, there might be a possibility to further improve the model if the exact corresponding information could be found for *D. ponderosa*. That could be the case also for development time, whose values are based on trees in sunny or shaded conditions for *I. typographus* and two different temperatures for *D. ponderosa*. Another aspect of model improvement would possibly be to modify the starting state of individuals of *D. ponderosa*. In contrast to *I. typographus* who normally hibernate as adult beetles, *D. ponderosa* more often hibernate as larvae, their least cold sensitive life stage (Karvemo and Schroeder 2010). That might lead to that the swarming and completion of generations is modeled to occur too early in this study.

6. Conclusion

As a consequence of climate change, the potential geographic extent and phenology of bark beetles will be altered. According to the models used in this study, by the end of this century, bark beetle populations will have expanded further north and to higher altitudes, and their bivoltine potential will be increased. Regarding Sweden, *I. typographus* will be able to successfully complete development of the first generation in almost the entire county by the end of the 21st century. In addition, a second generation will have the potential to develop in southern Sweden. *I. typographus* might consequentially imply a higher threat to Swedish and other European forest ecosystems in the future. According to climate conditions, *D. ponderosa* has the potential to establish in Europe. Due to its shorter development time, *D. ponderosa* even has a higher bivoltine potential than the native *I. typographus*. Therefore, *D. ponderosa* might potentially imply a threat to Swedish forests. However, the susceptibility of Swedish forest ecosystems and major tree species needs to be further investigated to draw deeper conclusion about the magnitude of that threat. To reduce the risk of future large scale attacks by *I. typographus*, *D. ponderosa* and other bark beetle species, foresters' need to continue to adapt to management practices that reduces the bark beetles outbreak potential.

7. References

- Amman, G. D. 1972. Some Factors Affecting Oviposition Behavior of the Mountain Pine Beetle. *Environmental Entomology*, 1: 691-695.
- Annala, E. 1969. Influence of Temperature upon the Development and Voltinism of *Ips typographus* (Coleoptera Scolytidae Picea-g-spp) Finland. *Annales Zoologici Fennici*, 6: 161-208.
- Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, 8: 1-16. DOI: 10.1046/j.1365-2486.2002.00451.x
- Bentz, B. J., and A. M. Jönsson. 2015. Modeling Bark Beetle Responses to Climate Change. In *Bark Beetles: Biology and Ecology of Native and Invasive Species*, ed. F. E. Vega. R. W. Hofstetter, 544-574. Academic Press
- Bentz, B. J., J. Regniere, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, et al. 2010. Climate Change and Bark Beetles of the Western United States and Canada: Direct and Indirect Effects. *Bioscience*, 60: 602-613. DOI: 10.1525/bio.2010.60.8.6
- Cognato, A. I. 2015. Biology, Systematics, and Evolution of *Ips*. In *Bark Beetles: Biology and Ecology of Native and Invasive Species*, ed. F. E. Vega. R. W. Hofstetter, 351-370. Academic press.
- Cullingham, C. I., J. E. K. Cooke, S. Dang, C. S. Davis, B. J. Cooke, and D. W. Coltman. 2011. Mountain pine beetle host-range expansion threatens the boreal forest. *Molecular Ecology*, 20: 2157-2171. DOI: 10.1111/j.1365-294X.2011.05086.x
- Euro-Cordex. EURO-CORDEX - Coordinated Downscaling Experiment - European Domain. Retrieved April 8 2015, from <http://www.euro-cordex.net/EURO-CORDEX.1908.0.html>.
- Faccoli, M. 2002. Winter mortality in sub-corticolous populations of *Ips typographus* (Coleoptera, Scolytidae) and its parasitoids in the south-eastern Alps. *Anzeiger Fur Schadlingskunde-Journal of Pest Science*, 75: 62-68. DOI: 10.1034/j.1399-5448.2002.02017.x
- Grégoire, J.-C., F. Kenneth, B. Raffa, and S. Lindgren. 2015. Economics and Politics of Bark Beetles. In *Bark Beetles: Biology and Ecology of Native and Invasive Species*, ed. F. E. V. a. R. W. Hofstetter, 585-613. Academic Press.
- Hall, M., E. Lund, M. Rummukainen, 2015. Klimatsäkrat Skåne. CEC Rapport Nr 02., Report, Centrum för miljö- och klimatforskning, Lunds universitet. [in Swedish, English summary]
- IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change., Report, Geneva, Switzerland.
- Jönsson, A. M., G. Appelberg, S. Harding, and L. Barring. 2009. Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle, *Ips typographus*. *Global Change Biology*, 15: 486-499. DOI: 10.1111/j.1365-2486.2008.01742.x
- Jönsson, A. M., S. Harding, L. Barring, and H. P. Ravn. 2007. Impact of climate change on the population dynamics of *Ips typographus* in southern Sweden. *Agricultural and Forest Meteorology*, 146: 70-81. DOI: 10.1016/j.agrformet.2007.05.006

- Jönsson, A. M., S. Harding, P. Krokene, H. Lange, A. Lindelow, B. Okland, H. P. Ravn, and L. M. Schroeder. 2011. Modelling the potential impact of global warming on *Ips typographus* voltinism and reproductive diapause. *Climatic Change*, 109: 695-718. DOI: 10.1007/s10584-011-0038-4
- Karlman, M. 2001. Risks associated with the introduction of *Pinus contorta* in northern Sweden with respect to pathogens. *Forest Ecology and Management*, 141: 97-105. DOI: 10.1016/s0378-1127(00)00492-8
- Karvemo, S., and L. M. Schroeder. 2010. A comparison of outbreak dynamics of the spruce bark beetle in Sweden and the mountain pine beetle in Canada (Curculionidae: Scolytinae). *Entomologisk Tidskrift*, 131: 215-224.
- Kirkendall, L. R., and M. Faccoli. 2010. Bark beetles and pinhole borers (Curculionidae, Scolytinae, Platypodinae) alien to Europe. *Zookeys*: 227-251. DOI: 10.3897/zookeys.56.529
- Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature*, 452: 987-990. DOI: 10.1038/nature06777
- Lange, H., B. Økland, and P. Krokene. 2006. Thresholds in the life cycle of the spruce bark beetle under climate change. *Interj. Complex Syst*, 1648.
- Lindgren, B. S., and K. F. Raffa. 2013. Evolution of tree killing in bark beetles (Coleoptera: Curculionidae): trade-offs between the maddening crowds and a sticky situation. *Canadian Entomologist*, 145: 471-495. DOI: 10.4039/tce.2013.27
- Marini, L., A. Lindelow, A. M. Jönsson, S. Wulff, and L. M. Schroeder. 2013. Population dynamics of the spruce bark beetle: a long-term study. *Oikos*, 122: 1768-1776. DOI: 10.1111/j.1600-0706.2013.00431.x
- McCambridge, W. F. 1971. Temperature Limits of Flight of Mountain Pine Beetle, *Dendroctonus ponderosae* Coleoptera-Scolytidae. *Annals of the Entomological Society of America*, 64: 534-&.
- Ministry of Forests, Lands and Natural Resources Operations. 2012. A History of the Battle Against the Mountain Pine Beetle. Retrieved April 8 2015, from https://www.for.gov.bc.ca/hfp/mountain_pine_beetle/Pine%20Beetle%20Response%20Brief%20History%20May%2023%202012.pdf.
- Powell, J. A., and B. J. Bentz. 2009. Connecting phenological predictions with population growth rates for mountain pine beetle, an outbreak insect. *Landscape Ecology*, 24: 657-672. DOI: 10.1007/s10980-009-9340-1
- Safranyik, L., and B. Wilson. 2006. *The Mountain Pine Beetle; A Synthesis of Biology, Management and Impacts on the Lodgepole Pine*. Victoria, BC, Canada: Pacific Forestry Centre.
- Samarasekera, G. D. N. G., N. V. Bartell, B. S. Lindgren, J. E. K. Cooke, C. S. Davis, P. M. A. James, D. W. Coltman, K. E. Mock, et al. 2012. Spatial genetic structure of the mountain pine beetle (*Dendroctonus ponderosae*) outbreak in western Canada: historical patterns and contemporary dispersal. *Molecular Ecology*, 21: 2931-2948. DOI: 10.1111/j.1365-294X.2012.05587.x
- Seidl, R., P. Baier, W. Rammer, A. Schopf, and M. J. Lexer. 2007. Modelling tree mortality by bark beetle infestation in Norway spruce forests. *Ecological Modelling*, 206: 383-399. DOI: 10.1016/j.ecolmodel.2007.04.002

- Six, D. L., and R. Bracewell. 2015. Dendroctonus. In *Bark Beetles: Biology and Ecology of Native and Invasive Species*, ed. F. E. V. a. R. W. Hofstetter, 305-350. Academic Press.
- Skogsstyrelsen. 2014. Genom att lära av Gudrun kan skogsskador hindras. Retrieved May 20 2015, from <http://www.skogsstyrelsen.se/Myndigheten/Nyheter/Nyhetsarkiv/Genom-att-lara-av-Gudrun-kan-skogsskador-hindras/>.
- SLU. 2015. Skogsmark. Retrieved May 20 2015, from <http://www.slu.se/sv/webbtjanster-miljoanalys/statistik-om-skog/skogsmark/>.
- Tauber, M. J., and C. A. Tauber. 1976. Insect Seasonality - Diapause Maintenance, Termination, and Postdiapause Development. *Annual Review of Entomology*, 21: 81-107. DOI: 10.1146/annurev.en.21.010176.000501
- Wermelinger, B. 2004. Ecology and management of the spruce bark beetle *Ips typographus* - a review of recent research. *Forest Ecology and Management*, 202: 67-82. DOI: 10.1016/j.foreco.2004.07.018
- Wilcke, R. A. I. 2015. Climate model selection for Potato Beetle study (*Unpublished*).
- Wood, S. L. 1982. The Bark Beetles and Ambrosia Beetles of North America and Central America Coleoptera Scolytidae a Taxonomic Monograph. *Great Basin Naturalist Memoirs*, 6: 1-1359.

Institutionen för naturgeografi och ekosystemvetenskap, Lunds Universitet.

Student examensarbete (Seminarieuppsatser). Uppsatserna finns tillgängliga på institutionens geobibliotek, Sölvegatan 12, 223 62 LUND. Serien startade 1985. Hela listan och själva uppsatserna är även tillgängliga på LUP student papers (www.nateko.lu.se/masterthesis) och via Geobiblioteket (www.geobib.lu.se)

The student thesis reports are available at the Geo-Library, Department of Physical Geography and Ecosystem Science, University of Lund, Sölvegatan 12, S-223 62 Lund, Sweden. Report series started 1985. The complete list and electronic versions are also electronic available at the LUP student papers (www.nateko.lu.se/masterthesis) and through the Geo-library (www.geobib.lu.se)

- 308 Nazar Jameel Khalid (2014) Urban Heat Island in Erbil City.
- 309 Jessica, Ahlgren & Sophie Rudbäck (2014) The development of GIS-usage in developed and undeveloped countries during 2005-2014: Tendencies, problems and limitations
- 310 Jenny Ahlstrand (2014) En jämförelse av två riskkarteringar av fosforförlust från jordbruksmark – Utförda med Ekologgruppens enkla verktyg och erosionsmodellen USPED
- 311 William Walker (2014) Planning Green Infrastructure Using Habitat Modelling. A Case Study of the Common Toad in Lomma Municipality
- 312 Christiana Marie Walcher (2014) Effects of methane and coastal erosion on subsea-permafrost and emissions
- 313 Anette Fast (2014) Konsekvenser av stigande havsnivå för ett kustsamhälle- en fallstudie av VA systemet i Beddingestrand
- 314 Maja Jensen (2014) Stubbrytningens klimatpåverkan. En studie av stubbrytningens kortsiktiga effekter på koldioxidbalansen i boreal barrskog
- 315 Emelie Norhagen (2014) Växters fenologiska svar på ett förändrat klimat - modellering av knoppsprickning för hägg, björk och asp i Skåne
- 316 Liisi Nõgu (2014) The effects of site preparation on carbon fluxes at two clear-cuts in southern Sweden
- 317 Julian Will (2014) Development of an automated matching algorithm to assess the quality of the OpenStreetMap road network - A case study in Göteborg, Sweden
- 318 Niklas Olén (2011) Water drainage from a Swedish waste treatment facility and the expected effect of climate change
- 319 Wösel Thoresen (2014) Burn the forest - Let it live. Identifying potential areas for controlled forest fires on Gotland using Geographic Information System
- 320 Jurgen van Tiggelen (2014) Assimilation of satellite data and in-situ data for the improvement of global radiation maps in the Netherlands.
- 321 Sam Khallaghi (2014) Posidonia Oceanica habitat mapping in shallow coastal waters along Losinj Island, Croatia using Geoeye-1 multispectral imagery.
- 322 Patrizia Vollmar (2014) The influence of climate and land cover on wildfire patterns in the conterminous United States
- 323 Marco Giljum (2014) Object-Based Classification of Vegetation at Stordalen Mire near Abisko by using High-Resolution Aerial Imagery

- 324 Marit Aalrust Ripel (2014) Natural hazards and farmers experience of climate change on highly populated Mount Elgon, Uganda
- 325 Benjamin Kayatz (2014) Modelling of nitrous oxide emissions from clover grass ley – wheat crop rotations in central eastern Germany - An application of DNDC
- 326 Maxime Rwaka (2014) An attempt to investigate the impact of 1994 Tutsi Genocide in Rwanda on Landscape using Remote Sensing and GIS analysis
- 327 Ruibin Xu (2014) Spatial analysis for the distribution of cells in tissue sections
- 328 Annabelle Finck (2014) Bird biodiversity in relation to forest composition in Sweden
- 329 Tetiana Svystun (2015) Modeling the potential impact of climate change on the distribution of Western Corn Rootworm in Europe”
- 330 Joel Forsmoo (2014) The European Corn Borer in Sweden: A Future Perspective Based on a Phenological Model Approach
- 331 Andrew Ekokwa Mwambo (2015) Estimation of Cropland Ecological Footprint within Danish Climate Commissions 2050 Scenarios for Land use and Bioenergy Consumption
- 332 Anna Lindstein (2015) Land- atmosphere exchange of carbon dioxide in a high Arctic fen: importance of wintertime fluxes
- 333 Karla Susana Markley Vergara (2015) Present and near future water availability for closing yield gaps in four crops in South America
- 334 Klara Århem & Fredrik Fredén (2015) Land cover change and its influence on soil erosion in the Mara region, Tanzania: Using satellite remote sensing and the Revised Universal Soil Loss Equation (RUSLE) to map land degradation between 1986 and 2013
- 335 Fei Lu (2015) Compute a Crowdedness Index on Historical GIS Data- A Case Study of Hög Parish, Sweden, 1812-1920
- 336 Lina Allesson (2015) Impact of photo-chemical processing of dissolved organic carbon on the bacterial respiratory quotient in aquatic ecosystems
- 337 Andreas Kiik (2015) Cartographic design of thematic polygons: a comparison using eye-movement metrics analysis
- 338 Iain Lednor (2015) Testing the robustness of the Plant Phenology Index to changes in temperature
- 339 Louise Hannon Bradshaw (2015) Submerged Landscapes - Locating Mesolithic settlements in Blekinge, Sweden
- 340 Elisabeth Maria Farrington (2015) The water crisis in Gaborone: Investigating the underlying factors resulting in the 'failure' of the Gaborone Dam, Botswana
- 341 Annie Forssblad (2015) Utvärdering av miljöersättning för odlingslandskapets värdefulla träd
- 342 Iris Behrens, Linn Gardell (2015) Water quality in Apac-, Mbale- & Lira district, Uganda - A field study evaluating problems and suitable solutions
- 343 Linnéa Larsson (2015) Analys av framtida översvänningsrisker i Malmö - En fallstudie av Castellums fastigheter
- 344 Ida Pettersson (2015) Comparing Ips Typographus and Dendroctonus ponderosus responses to climate change with the use of phenology models